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A General Ecology of Bryozoans
at Signy Island, Antarctica

A Thesis Submitted in Accordance with the Requirements of the
Open University for the degree of

Doctor of Philosophy.

By

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Abstract

This study set out to investigate a broad range of ecological aspects in Antarctic bryozoans, including distribution, feeding, growth and predation, and how these were influenced by environmental conditions. A number of sites, at a variety of depths, were chosen from within Borge Bay, Signy Island in the South Orkneys, using SCUBA. Some of these studies attempted to monitor populations in situ over the course of two years, mainly with the aid of underwater cameras.

Photographic samples were taken on three vertical transects of 5.5 m rock faces and two 40 m sloping transects. The percentage cover of substratum ranged from 0-100% and the colonising communities included representatives of 10 phyla. Ice impact, depth and profile were important influences on community cover and composition. Collections of up to 200 rocks were made from each of six localities ranging from the intertidal to 42 m. Area colonised, number of colonising phyla, bryozoan species and colonies were all found to increase with substratum surface area and depth. Over 4000 competitive interactions between bryozoans were recorded, which indicated the presence of a competitive hierarchy with one ultimately dominant species. Colonisation of artificial substrata was very slow comparative to that found by similar temperate studies and suggested an essentially classical successional pattern of colonisation. Bryozoans were abundant on the externa of a variety of other macroinvertebrates, including fouling the surfaces of erect bryozoan species.

Lophophore activity (feeding) occurred for most of the year in the bryozoans monitored, and environmental cues were suggested for the changes in activity of some species. Growth was generally slow but contrasted strongly in duration between the monitored species. The growth checks, formed annually by one species, showed interannual variations in growth throughout the population. Two bryozoan species had specific nudibranch predators, though their populations seemed little influenced by predation.

Acknowledgements

As with more than a few theses, the final product bore no resemblance to the original plans and on several occasions it seemed as though everything had gone horribly wrong. So, more than anyone, I have to thank my supervisor Andy Clarke for keeping me on the straight and narrow, trying to decipher my coded communications from base and improving my writing style from extreme brevity to merely short. The entire base knew when a work dive hadn't achieved the aim, and many nights had many heads around the bar trying to solve problems. So enormous thanks go to everyone on Signy base between November 1990 and March 1993, especially the diving officers Greg Wilkinson (Pog), Derek Gittins and Rob Wood, the boatmen Pete Macko and Russ Manning and the marine assistants Luke Bullough and Simon Brockington. I would like to thank the radio operator Roy Glover for incredibly - cannibalising my two broken underwater strobes and building a working one saving a month's data and everybody who at some point stood out in the cold holding the rope for underice dives. I particularly have to thank Pog for bringing me up from 38 m when my demand valve first stage failed and on a separate occasion pulling me out of the water when our skidoo went through thin ice. It is nice to still be around, cheers Pog.

Throughout the project I had crises of identification and each time Peter Hayward, my external supervisor was able to quickly reassure or correct taxonomic problems, for which I am very grateful. During the analysis, interpretation and writing up of studies I have had tremendous support from Lloyd Peck, Peter Rothery, Stefan Hain, Sara Lawrence, Lucy Conway, Andy Wood, the drawing office team of Roger Missing and Tony Sylvester and of course again Andy Clarke. Various people from other institutes have provided key help with identification of various associated organisms, and I would like to especially thank Heike Wägele, Ole Tendal and Julian Gutt.

Finally thanks to my family, friends and Jo for staying with me and writing during the 29 months I was fortunate enough to be on Signy Base. I've never found anywhere more difficult to leave and I think I will be lucky if I experience another two years as memorable as those on Signy, its closure is difficult to accept.

Section 1. General Introduction

A brief history of marine research in Antarctica

Science in Antarctica began, at a rudimentary level, over 200 years ago during James Cook's circumnavigation, with general observations and a few biological investigations. In the early nineteenth century, a short period after this voyage and those of subsequent sealers and whalers, a number of governments initiated scientific expeditions to the Southern Ocean and the shores of the Antarctic continent. James Eights, on an American expedition, provided some of the first marine benthos collections and descriptions, including characteristic species such as the giant isopod *Glyptonotus antarcticus* (1835).

Collections of benthos from the South Orkney Islands and other sub-Antarctic island groups were made during the late 1830s and early 1840s, by the French expedition led by Dumont d'Urville and the American expedition of Charles Wilkes. At a similar time period the British expedition of Sir James Clark Ross collected bryozoans amongst other benthic taxa, which were later described by Stokes (1847). It was the *Challenger* expedition from 1872-1876, however, which really began southern ocean marine science in earnest, again focussing on the islands of the sub-Antarctic.

At the turn of the century two expeditions provided comprehensive collections of benthic fauna and subsequently produced two monographs on the bryozoans encountered (Waters 1904, Calvet 1909), which still stand as the authority for some species today. The collections made by these Belgian and French voyages were from the coast of the actual Antarctic continent and particularly illustrated the high degree of endemism of the fauna. There were also important contributions to marine science from the German expedition of 1901-1903 and two British expeditions which preceded the First World War, which postponed further Antarctic operations.

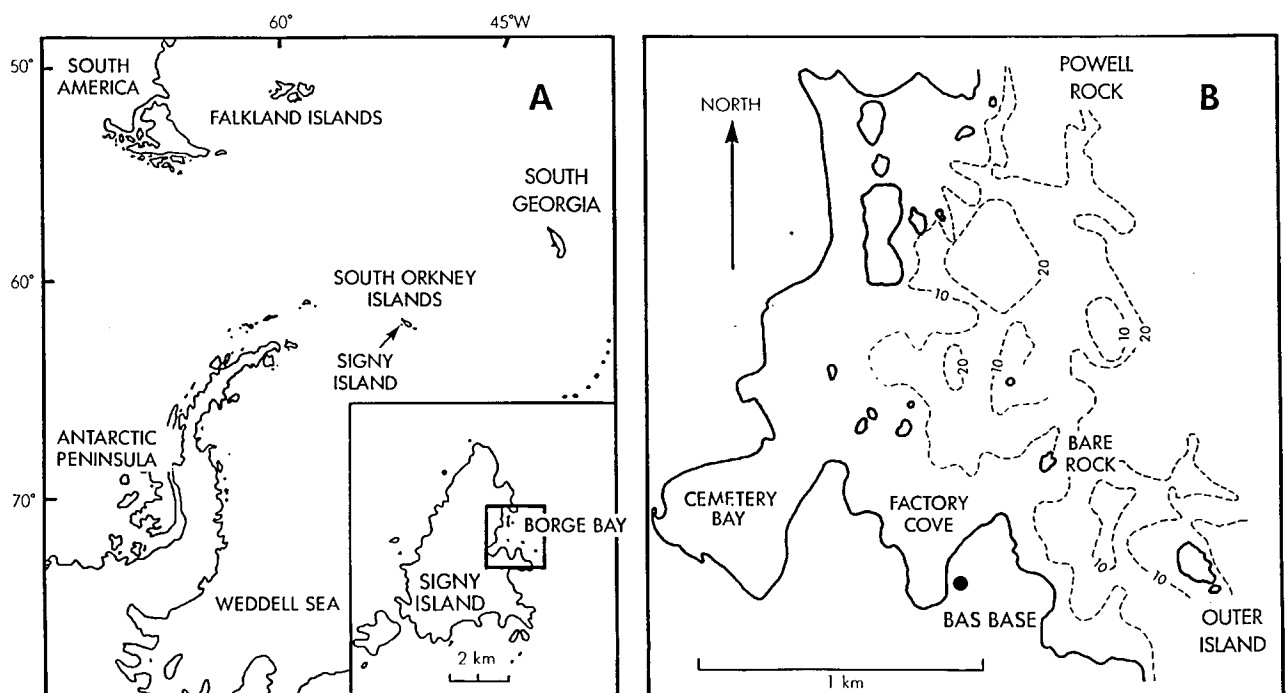
From 1925-1939 the *Discovery* expeditions were to produce a massive and, for the time, still incredibly comprehensive collection of specimens and data, such that examples would still be worked on by taxonomists into the 1990s. But ships were already beginning to support more than just scientific cruises. The close of the second world war saw a

number of nations setting up permanently manned bases on the continent and its outlying islands. Relief and re-supply of bases became an important function of voyages to the Antarctic so that science could now run continuously. The development of SCUBA techniques for polar waters has also created new opportunities to observe, collect and experiment with marine organisms and has been fundamental in inshore coastal programs.

Headland's (1989) chronological list of Antarctic expeditions shows the explosion of scientific and political interest in the Antarctic continent and surrounding waters since Cook's circumnavigation. Monographs have been published periodically documenting historical and biological information of marine studies (Dell 1972, White 1984, Dayton 1990) and reviews of marine polar science are now published almost annually (Arntz *et al.* 1994). With commercial pressures and exploitation of Antarctic waters an ever increasing threat, biological monitoring and understanding become more important than ever.

Figure 1.1

(A) The position of Signy Island and other island groups of the Scotia Arc in the South Atlantic, insert: Signy Island showing position of Borge Bay (B) Details of study site locations and depth contours in Borge Bay



Signy Island and the research station

Signy Island is a small, partly glacier covered island in the South Orkney Islands which lie south-east of the Falkland Islands and Patagonia, and north-west of the Antarctic Peninsula (Fig. 1.1). The South Orkney Islands in the maritime Antarctic, together with the South Sandwich and South Shetland Islands, form part of the chain of mountains (the Scotia arc) linking the Andes with the Antarctic Peninsula (Fig. 1.1 A). Most of the mountains in the Scotia Arc are subsurface. As with some parts of the peninsula and continental mainland, Signy Island is north of the Antarctic circle ($60^{\circ}43'S$, $45^{\circ}36'W$), but is south of the southern oceanographic barrier, the Polar Frontal Zone (Clarke & Crame 1989). The temperatures and ice conditions experienced around Signy Island reflect its position south of the Polar Frontal Zone, but are often colder than western parts of the peninsula further south because of the influence of circumpolar currents. Cold water from the Weddell Sea flows up the east side of the Antarctic peninsula and, restricted by bathymetry (meeting the Scotia arc), continues past the South Orkney Islands and around the Antarctic continent warming slightly on route. The air temperatures at Signy vary around $1^{\circ}C$ in summer and $-15^{\circ}C$ in winter.

The metamorphic rocks of Signy Island are in places covered by mosses, lichens and two species of flowering plant. A growing population of about 15,000 non-breeding fur seals are seasonal visitors along with smaller numbers of elephant, leopard, crabeater and weddell seals. Amongst the 13 species of sea birds resident, is a summer penguin population of about 300 000 individuals. Small mites, insects and tardigrades are the largest truly terrestrial animals.

The biological research station (Fig 1.2) is situated on the east coast of Signy Island (Fig. 1.1 A inset), by Factory Cove. Working sites were selected around Borge Bay (Fig. 1.1 B) in which a wide range of depths and marine conditions occur. The field work involved an unbroken 28 month period of stay on the research station together with a team of 12 other scientists and support personnel. Most of the work was carried out using SCUBA from inflatable boats or RIBs (Rigid Inflatable Boats), although occasional trawls

were carried out using the launch *Pomona*, which was also based at the station. The station was resupplied by the ships RRS *Bransfield* and RRS *James Clark Ross* each November and the station team would temporarily expand to 27 from November until March.

The nearshore Antarctic marine environment

Low temperature and intense seasonality of primary production characterise the Southern Ocean marine ecosystem. It is an environment of strongly contrasting physical parameters, with relatively small fluctuations in some (for example temperature and salinity) and a marked seasonal variation in others (for example chlorophyll standing stock: Clarke *et al.* 1988). The large seasonal variation in light climate, exacerbated by the winter ice cover, leads to a short but intense period of primary production (Whitaker 1982). This production is dominated by larger diatoms and imposes a strong seasonal variation in food availability for herbivores (Clarke 1988). For shallow water benthos in high southern latitudes there would thus appear to be a large seasonal difference between the summer period characterised by intense productivity, disturbance by currents, wave action and occasional ice-scour, and a longer period of very low food availability, low light and minimal disturbance.

Figure 1.2

The research station at Factory Cove, Signy Island



Whilst being fairly typical of the above conditions, the marine environment of Borge Bay, Signy Island in the maritime Antarctic, has additional local and nearshore influences. The position of Signy Island close to the northern edge of the Weddell Sea gyre means that there are large interannual variations superimposed on the seasonal cycle of seawater temperature, ice cover and chlorophyll standing crop (Murphy *et al.* in press). The sea water temperature regime fluctuates between a winter minimum of approximately -1.8°C and a summer maximum of approximately $+0.5^{\circ}\text{C}$, although occasionally local under-ice salinity may allow winter supercooling to -2°C . Fast-ice may form quicker and last longer in small sheltered inshore bays, such as Factory Cove in Borge Bay, than in deeper water. Thus ice may be thicker here and consequently subsurface light and disturbance levels lower. Fresh water run off from land and ice melts in spring may decrease the surface salinity of small inshore bays, but the salinity usually varies little from a mean of 33.91‰ (Clarke *et al.* 1988). The mean duration of fast ice is about 140 days (measured between 1969 and 1994), although year to year variation is high. The peak chlorophyll concentrations of the nearshore waters of Borge Bay may be even more intense than those of open ocean, occasionally reaching 50.9 mg/m^3 , although these too have large interannual variability (Clarke *et al.* 1988). During the open water (summer) period icebergs regularly drift into Borge Bay and ground on or scour localised areas of rock or sediment.

The intertidal environment is fast-ice covered in winter and characterised during the summer by strong disturbance from wave action and scouring from water borne pieces of ice, as well as large fluctuations in temperature and salinity.

The shelf and sublittoral benthos of Antarctica

At many of the locations on the Antarctic continental shelf which have been examined, rich, predominantly sessile, benthic communities have been found (Belyaev & Ushakov 1957, Tressler 1964, Propp 1970, Knox 1970, Voß 1988, Galéron *et al.* 1992). The biomass and abundance of Antarctic marine benthos, although much greater in some locations (Dell 1972) than others (Gallardo & Castillo 1969), is generally thought to be

relatively high on both hard and soft substrata (White 1984, Clarke & Crame 1989, Clarke 1990). The biomass levels, such as 1kg/m^2 at 25-30 m depth (Propp 1970) and 6kg/m^2 at 45-50 m depth (Andriashev 1968), found by Russian divers were comparatively high for these depths in global terms. Certain sublittoral habitats within Borge Bay, Signy Island have been estimated to contain biomasses in excess of 4kg/m^2 (White & Robins 1972). Adaptation to seasonal food availability and, low metabolic rates are thought to be the principal factors responsible for the high benthic standing crop (Brey & Clarke 1993). While certain taxa are poorly represented or absent in south polar waters, most notably the decapod crustaceans, the general species diversity of benthic groups is high (Brey *et al.* 1994).

Figure 1.3

Dense benthos at 20 m on a vertical rock face, Powell Rock, Signy Island.



Sessile suspension feeders often dominate or constitute an important part of Antarctic benthic shelf communities (Knox 1970, Winston & Heimberg 1988, Galéron *et al.* 1992) particularly above 500 m depth (Belyaev 1958, Uschakov 1963). Of these sessile or vagile suspension feeding groups, sponges, ascidians, holothurians and bryozoans have been found to be the most abundant in terms of biomass (Winston & Heimberg 1988) and area occupation (Barnes 1995a,b). The Antarctic benthic environment is among the richest anywhere known for diversity and abundance of the lophophorate phyla, bryozoans (Winston 1983) and brachiopods (Foster 1974). These assemblages may occur as shallow as the sublittoral in the maritime Antarctic, for example at Signy Island (chapters 2,3,4, White & Robins 1972, Barnes 1995a,b) and King George Island (Rauschert 1986).

Many Antarctic sublittoral locations that have been studied, however, have been described as largely devoid of life. Anchor ice, formed when supercooled water nucleates around sublittoral objects and the ice so formed subsequently grows until the buoyancy tears away the object, has been described as responsible for the impoverishment and zonation of high Antarctic sublittoral benthos (Dayton *et al.* 1970, 1974). Iceberg scour may also be a strong influence on community development in the sublittoral, particularly in the maritime Antarctic where long periods of open water allow considerable ice movement (Peck & Bullough 1993).

General taxonomy and biology of bryozoans

The phylum Bryozoa comprises about 4300 known species today, but with a prolific fossil history of almost five times this number of species (Barnes, Calow & Olive 1993). They have in common with two other phyla a distinctive feeding apparatus termed the lophophore, which is essentially a ring of tentacles which surrounds the mouth but not the anus, and a tripartite body plan. The taxonomic importance of these structures remains disputed and the phylogenies of the three lophophorate phyla, bryozoans, brachiopods and phoronids, are uncertain. Entoprocts, a superficially similar phylum of animals but which lack a lophophore, have many affinities with bryozoans and have often been linked in ancestry with bryozoans (see review by Barnes, Calow & Olive 1993). The histolysis of

tissues during metamorphosis of the settled larva, and subsequent reorganisation into adult tissues, leaves the body cavity and the deuterostome nature of the phylum debateable.

Bryozoans are entirely colonial, with colonies consisting of a few to a few million clonally budded modular units termed zooids. Within the skeletal box or zooecium of each zooid is the polypide, which may suspension feed by everting the lophophore from inside the zooecium. The lifespan of each polypide is short relative to that of the colony, and there may be several generations of polypides produced in each zooecium. This is achieved by degeneration and regeneration (Gordon 1977, Dyrinda 1981). All the polypide remnants which are not able to be reabsorbed by the colony form a small sac termed 'brown body', several of which may accumulate within a zooecium after a number of generations (Ryland 1976). Bryozoan colonies are hermaphrodite, with gonads that rupture into the metacoel and may be released through coelomopores. The eggs cleave radially, are usually brooded to give rise to lecithotrophic larvae. The larvae settle after a variable length of time to form the first zooid, termed the ancestrula, which then produces a young colony by subsequently budding zooids asexually.

Both colonies and zooids illustrate a wide variety of form. Although the colonies of most bryozoan species are encrusting, some become foliaceous or erect and flexible and some species have a large, heavily calcified, erect and "rooted" form (McKinney & Jackson 1991). Zooids, particularly in the order cheilostomatida, have a wide variety of form and function (Reed 1991). Deviations from the basic feeding autozooid, include specialisation for reproduction, defense, cleaning and anchorage and in erect colonies for support (see Silen 1977). The evolution and diversity of form in one such specialization, the avicularium, was commented on by Darwin (1859) to illustrate certain points in his new theory of natural selection. In some cheilostome species, the operculum or trap door which allows the lophophore to be everted from the zooid, has become greatly thickened, enlarged and elongated in some zooids, whilst their polypides dwindled to become vestigial. The purpose of these avicularia is still uncertain in many species although a colony defense function has been postulated in some (Winston 1984, 1986) and a cleaning function in others (Winston 1991, Barnes 1994).

The phylum is divided into three classes, the freshwater Phylactolaemata, the mostly marine Gymnolaemata and the entirely marine Stenolaemata. The Gymnolaemata, which constitutes about three quarters of all living bryozoan species and the majority of known Antarctic bryozoans, is comprised of the two orders: Ctenostomatida and Cheilostomatida. The Cheilostomata were the central taxon to this study and, as described above, are characterised by high diversity of both colony and zooid form.

Antarctic bryozoans

The ecology of Antarctic bryozoans has recently been described as "...a virtually untouched field." (Hayward & Taylor 1984) and "...the ecology and physiology of feeding in Antarctic Bryozoa remain a complete mystery." (Sanderson *et al.* 1994). Although bryozoans have been found to be an important component of the Antarctic suspension feeding communities, until recently the Antarctic bryozoan fauna remained little known. Some Antarctic and sub Antarctic species are still only known from the early expeditions (Waters 1904, Calvet 1909, Rogick 1965), although many have now been revised and new species described (Hayward & Thorpe 1987, 1988a, b, c, d, 1989a, b, 1990, Hayward & Ryland 1990, Hayward 1991, 1992, 1993, Hayward & Winston 1994). These recent advances in the taxonomy of polar bryozoans have facilitated new studies into various aspects of bryozoan ecology, notably feeding (Sanderson *et al.* 1994, Barnes & Clarke 1994, 1995a) and community distribution and dynamics (Barnes 1995a,b, Barnes & Clarke 1995b, Barnes *et al.* in press).

Cheilostome bryozoans, in particular, have now been established as abundant and diverse in Antarctic waters, forming 85% of the 222 bryozoan species found by the United States Antarctic Research Program (Winston & Hayward 1993). Winston (1983) has described large populations of cheilostomatid bryozoans from Antarctic waters and nearly 200 species have been described which are endemic to the Antarctic (Rogick 1965). The few studies of Antarctic bryozoans to date have relied on collections, and the scant ecological knowledge gained before this study has been inferred from trawled collections or observations of a few living specimens in aquaria (Winston 1983, Moyano 1984,

Winston & Bernheimer 1986, Winston & Heimberg 1988, Sanderson *et al.* 1994).

The proportion of cheilostome bryozoans described from Antarctic regions is high compared with other areas studied. Furthermore Hayward & Thorpe (1989) suggest that considering the unusual ratio of species' numbers so far discovered in two of the cheilostomatid suborders, the Ascophora and Anasca, many species may remain to be found and described from the Southern Ocean. The cheilostomatid species described from Antarctic waters to date encompass many erect forms, including some of the largest known. At present it is unclear, however, whether the relatively low described abundance of small and encrusting species is real or a reflection of sample bias and the lack of comprehensive studies.

In total over 50 cheilostome bryozoan species were examined in this study, although fewer than ten were involved in the detailed investigations. Four broad morphological groupings described all the species involved in this study, most of which were of the encrusting growth form. The largest individuals in terms of size or mass were the foliaceous (encrusting massive) forms, sometimes reaching over a metre in diameter and supporting extensive micro-communities. Such morphologies are the most obvious bryozoans to the casual SCUBA observer at Signy Island (illustrated dominating a rock face in figure 1.2). Flexibly erect forms, resembling small fans or algae, were examined in particular detail because of their ease of removal from substrate, more determinate growth form, but mainly because they could be monitored photographically with minimal disturbance. The fourth and rarest growth form (within SCUBA range) were the heavily calcified, rigid erect forms. Such forms develop kenozooidal rootlets (as means of support) and many displayed external rings.

SCUBA as a tool for research in Antarctic waters

The profile of and the science undertaken by organisations in the Antarctic has increased dramatically over the last decade. The improvement in international cooperation and technical facilities have constantly increased the boundaries of scope for scientific

investigations. This is particularly apparent for marine life science studies using SCUBA. The research station at Signy Island run by the British Antarctic Survey is still only one of four or five bases in the Antarctic with a year round SCUBA facility. The total number of dives carried out annually from Signy Base, however, has increased four fold over the last decade to over 600 per year at present time.

The suits and breathing apparatus used by divers of the British Antarctic Survey are much as is used for cold water SCUBA diving in temperate regions, such as the U.K. in winter. For much of the austral year the air and sea temperature both fall below 0°C, requiring particular care of equipment and awareness of potential problems associated with the temperatures. Of the 477 dives carried out at Signy Island, for this study, the seasonally frozen sea surface or fast ice acted as a platform for a third. Under-ice' diving necessitated over ice travel, usually by snowmobile and sledge, and the cutting of an entry hole large enough for the dive pair to exit together. A rope is tied to one of the divers and reeled out from the surface by a linesman; this is important for the divers to navigate back to the hole and for emergency recall. In the early weeks or possibly months of the sea freezing, such holes may be created using an axe, but a chainsaw or ice drill is soon required as the ice thickens and hardens. Once fast-ice is present the visibility in the water column increases from a summer minimum of two metres or less, to in excess of 50 m. The benefits of winter diving, in addition to visibility, are access to sites over a wider range of weather conditions and surface marking of sites by dive holes. Offset against these benefits, however, are the lower temperatures and higher rate of equipment failure, particularly chainsaws, in the colder conditions.

Although there is a decompression chamber within Signy base, the British Antarctic Survey require the duration of all Antarctic dives to be within no stop times of RNPL tables (no in-water decompression). This means that deeper dives are very brief and the work undertaken underwater must be highly efficient. Over 42% of the dives involved in this study took place at depths between 30 - 48 m. At these depths the proportion of successful dives (those which achieved their aim) totalled 69%, substantially lower than the success rate of 95% from dives shallower than 30 m.

Objectives

The general ecology of temperate and tropical bryozoans has been widely investigated since the 1970s, particularly with respect to aspects of feeding and competition. Transects and mapping surveys using SCUBA have examined the distribution and abundance of bryozoans relative to other benthos in the sublittoral zone. The ecology of bryozoans in the Southern Ocean, 10% of the world's ocean area, has remained unknown, despite the knowledge of the existence of prolific benthic assemblages rich in bryozoans. This thesis intends to address some of the major aspects of ecology in Antarctic bryozoans.

The first section of this thesis examines the broad distribution and abundance of bryozoans as a taxon, with respect to other encrusting benthos, around Signy Island. As well as colonising primary substratum such as rock, the importance of bryozoans as fouling agents of other organisms, including erect bryozoans was investigated. The duration and sequence of colonisation was looked at experimentally using settlement plates. Following recruitment the ensuing growth, competition and dispersal were studied on natural substrata in a range of size classes and depths. These studies built up an overview of the ecological position occupied by Antarctic bryozoans as a taxonomic group in relation to other local benthos.

The second section of the thesis concentrates more on specific examples of the bryozoan fauna and their systematics *in situ*. The general feeding ecology of 10 common species of differing morphologies and habitats are compared with representatives of some other suspension feeding groups. A more detailed examination of four bryozoan species was also undertaken, two of which were also monitored periodically for measurements of growth. The study of a heavily calcified erect species, which formed growth check lines, made measurements of annual as well as seasonal growth variability, possible. The last chapter investigates bryozoan predation, by examination of the ecology of one of the major groups of bryozoan predators; the nudibranch molluscs.

Overall this thesis provides a first and broad examination of Antarctic bryozoan

ecology, in relation to other local benthic suspension feeders. Many aspects of the study were, in contrast to many cold water marine studies, undertaken *in situ* allowing an undisturbed and direct view of this particular phylum of animals.

Figure 1.4

Holes are cut in the sea-ice to continue underwater work during the austral winter



Section 2. Distribution

Sublittoral epifaunal communities : The ice foot zone

Introduction

Distribution patterns of Antarctic benthos were first studied in the Ross Sea (Bullivant & Dearborn 1967), more recent studies in the Davis Sea have shown substratum to be one of the most important factors affecting the distribution and abundance of macrobenthic species, although depth, slope and current amongst other factors are also involved (Kirkwood & Burton 1988). Studies of the upper sublittoral (for review see Arntz *et al.* 1994) also found that the presence and the thickness of icesheets, and the resulting light attenuation, were important in the development of benthos. The sublittoral benthos, which was absent from the top 7-8 m, consisted mostly of sparse algae and vagile echinoderms (Gruzov & Pushkin 1970). In the intertidal and sublittoral regions fauna is usually scarce (Propp 1970, Hedgpeth 1971, Zamorano 1983, Dayton 1990, Arnaud 1992), but in some locations, such as Signy Island, dense faunal assemblages may occur as shallow as 10 m (White & Robins 1972). In the high Antarctic, below the generally impoverished sublittoral, marked zonation of benthos has been described (Gruzov 1977, Zamorano 1983, Dayton 1990).

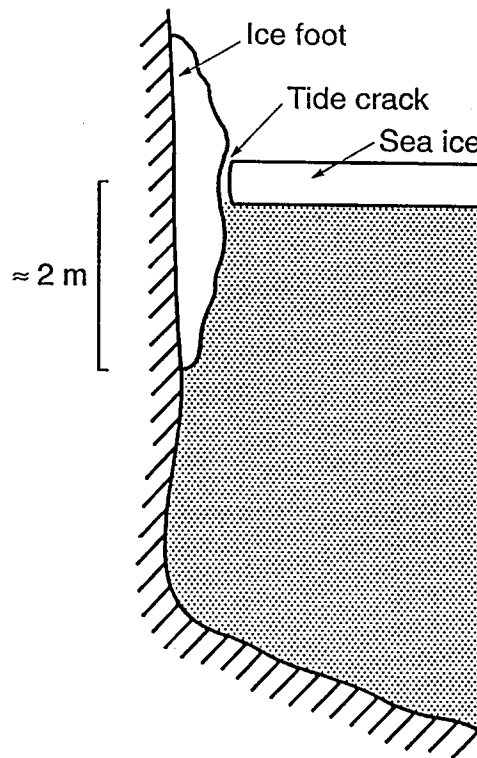
Anchor ice is one factor responsible for the scarcity of fauna in shallow Antarctic water, and for the zonation to depths of 30 m, particularly in high Antarctic areas (Dayton *et al.* 1970, 1974, Zamorano 1983). However, a study at King George Island, north of the main continent and in the maritime Antarctic zone, suggested that ice had a strongly adverse effect only down to 4 m (Rauschert 1991). In many polar areas the formation of winter fast ice (sea ice), and the subsequent tidal movement of this ice usually leads to the build up of ice around the intertidal zone (Fig. 2.1), often referred to as the ice foot (Kotlyakov & Smolyarova 1990). At Signy Island the tidal range is approximately 2.5 m during spring tides and 1.5 m during neap tides. The thickness of the ice foot, which in places reaches several metres, corresponds to a vertical height slightly greater than the tidal range. This obviously exerts a major influence on benthic life within the intertidal and shallow sublittoral. The benthic communities on soft substratum may also be affected or

entirely removed by iceberg scour (Richardson & Hedgpeth 1977, Peck & Bullough 1993).

This chapter describes the hard substratum communities of vertical rock faces in the ice foot zone (0 to 5.5 m) at Signy Island, Antarctica, and chapter 3 examines the epifaunal communities over a broader depth range in the sublittoral (0 to 40 m). The first of these two studies, reported in this chapter used quadrats of a smaller area, over smaller depth increments and a smaller depth range in order to achieve a greater level of detail than in the study of depths below the ice foot zone. A higher degree of detail could be achieved only in the shallow water depths because of the time constraints of SCUBA operations. Although the techniques used in this chapter and chapter 3 were different, they were in most respects comparable. These studies form part of a broad ecological investigation into the Antarctic bryozoan distribution and abundance. The main aims of this study were to investigate the impact of ice on the distribution and taxonomic composition of upper sublittoral hard substratum communities.

Figure 2.1

A vertical rock face with the ice foot associated with fast ice. Tidal water movement creates a gap between ice foot and fast ice known as a 'tide crack'.



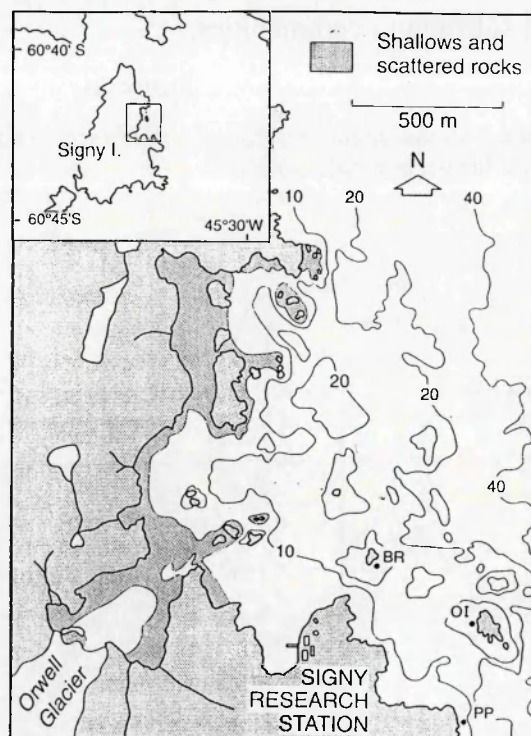
Materials and methods

Study site and species

This study was undertaken at Outer Island, Bare Rock and Polynesia Point, close to the British Antarctic Survey research station at Signy Island, South Orkney Islands ($60^{\circ}43'S$, $45^{\circ}36'W$). These sites all occur within Borge Bay, for which a long term database of environmental variables, including sea temperature, ice cover and chlorophyll standing crop, has been established (Whitaker 1982, Clarke *et al.* 1988, Leakey *et al.* 1994). The location of the study sites is shown in Figure 2.2.

Figure 2.2

Map of Signy Island showing position of study sites (OI Outer Island, BR Bare Rock, PP Polynesia Point). Depth contour lines (m) are also shown.



Each site is characterised by an approximately vertical rock face from the low water neap tide level to between 5 and 5.5 m depth, after which there is a shallow gradient. The exposure of each of the sites to ice foot formation and wave action is thus broadly similar. The winter sea ice typically reaches a maximum of 1 m in thickness (Clarke *et al.* 1988), but the associated ice foot may become more than twice as thick on vertical faces, such

as occurred at these three locations (Fig. 2.1). The duration of the ice foot (and other disturbances created by ice or water) is obviously linked to sea ice duration. This is highly variable at Signy, being linked to regional scale processes in the Weddell Sea (Murphy *et al.* in press). Records made at Signy research station since 1947 indicated a median duration of 140 days, with a range of 0 (1956) to 219 (1966) days (Clarke *et al.* 1988, Murphy *et al.* in press).

Table 2.1

Bryozoan species identified within the sampled areas of the transects. The species with a corresponding + were grouped together, along with a number of unidentified species, as these could not be confidently separated in terms of area occupied at the level of resolution used in this survey.

Species identified in transects	
<i>Celleporella bougainvillei</i> (d'Orbigny)	
<i>Inversiula nutrix</i> Jullien	
<i>Escharoides tridens</i> (Calvet)	
<i>Arachnopusia inchoata</i> Hayward & Thorpe	
<i>Beania erecta</i> Waters	
<i>Ellisina antarctica</i> Hastings	+
<i>Micropora brevissima</i> Hayward & Taylor	+

Various species of macroalgae were encountered, but for the purposes of this study they were not separated into species. The level of taxonomic resolution achieved varied between animal groups, largely dictated by existing taxonomic knowledge. The Porifera, Annelida and Cnidaria were treated simply as phyla, whereas the Bryozoa were analysed to species, all other phyla were summed together, due to different levels of abundance. The species of Bryozoa identified in this study are listed in table 2.1.

Transects and measurement

The field work of this study took place over the austral summer of 1991/1992, and the analysis was undertaken during the subsequent austral winter. At each site four or five photographs were taken every 0.5 m along transect lines running from mean low water

neap tide level to either 5 or 5.5 m depth. Each photograph covered an area of 24cm x 17cm. Occasionally areas within these quadrats were photographed at higher resolution, using extension tubes, to give an approximately life size replication to aid identification. Fujichrome 50 ASA colour reversal film was used. This was developed at Signy island and projected onto a screen composed of 7700 dots in a regular grid. The area occupied by the base of each group was assessed by counting the number of dots covered and dividing this into the total area of the photograph to give percentage figures. An overall mean was calculated for each set of replicates. This technique has been shown to give results indistinguishable from other randomised dot methods or visual estimation for species covering $\geq 30\%$ area, but may fail to detect species covering $\leq 1\%$ area (Meese & Tomich 1992). Site profiles were also noted.

Within the quadrats examined, interactions between encrusting phyla were recorded. Overgrowth was defined as the protrusion of the growth margin of one competitor over that of the other. This definition of overgrowth made application to phyla with very small areas of substratum contact, such as entoprocts, brachiopods and hydroids, difficult. The overgrowth data are thus presented only for taxa with encrusting growth form, namely some bryozoans, sponges and ascidians.

Results

The impact of the winter ice foot was apparent in that the substratum was devoid of encrusting organisms for the first metre and a half below mean low-water neap tides. During ice-free summer periods, however, transient populations of mobile animals, mostly amphipods and the Antarctic limpet *Nacella concinna* (Walker 1972, Davenport 1988, Nolan 1991), occurred within this region. Below this depth a number of species of algae became abundant, and at 3.5 m animal groups began to dominate the communities. The profiles of the three transects and the relative areas occupied by each group are shown in Figures 2.3a, b & c. At 5 m depth a number of other animal groups, as well as the seven sessile phyla recorded in this study, were abundant. These vagile or errant animals,

Figure 2.3a

The substratum profile, with depths and associated histograms (scaled 0 to 100% cover), of the transect at Outer Island. Zero depth datum corresponds approximately to mean low water level. (Taxa = B bare rock; L, (probably) *Lithothamnion* sp.; H (probably) *Hildenbrandia* sp.; M, macroalgae; P = Porifera; A, Annelida; N, Cnidaria; U, Urochordata and other minor colonising phyla; bryozoans = I, *Inversiula nutrix*; C, *Celleporella bougainvillei*; E, *Escharoides tridens*; Ar, *Arachnopusia inchoata*; B, *Beania erecta*; O, other encrusting species)



Figure 2.3b

The substratum profile with depths and associated histograms (scaled 0 to 100% cover) of transects at Bare Rock. Zero depth datum corresponds approximately to mean low-water level. (Taxa = B bare rock; L, (probably) *Lithothamnion* sp.; H (probably) *Hildenbrandia* sp.; M, macroalgae; P = Porifera; A, Annelida; N, Cnidaria; U, Urochordata and other minor colonising phyla; bryozoans = I, *Inversiula nutrix*; C, *Celleporella bougainvillei*; E, *Escharoides tridens*; Ar, *Arachnopusia inchoata*; B, *Beania erecta*; O, other encrusting species)

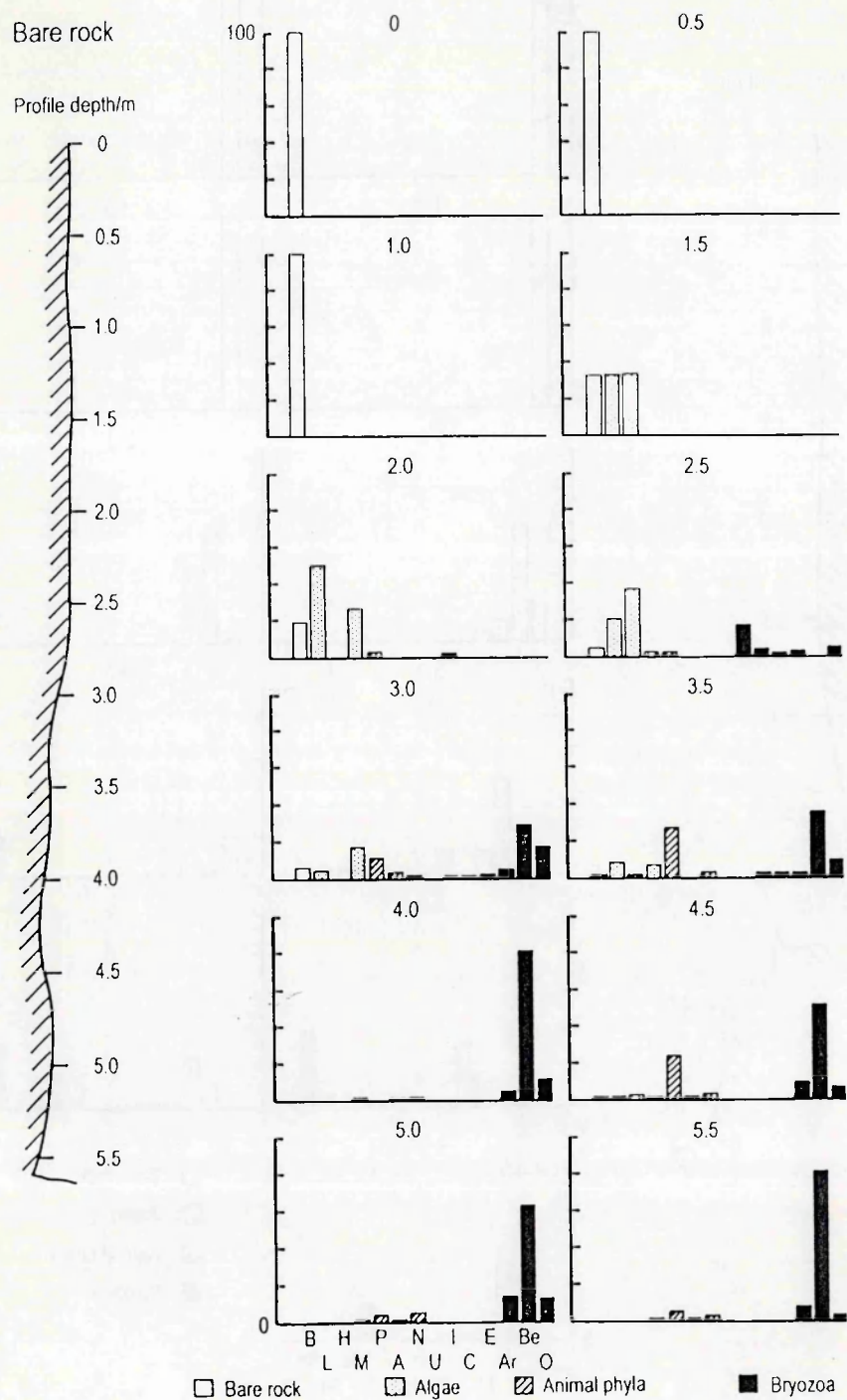
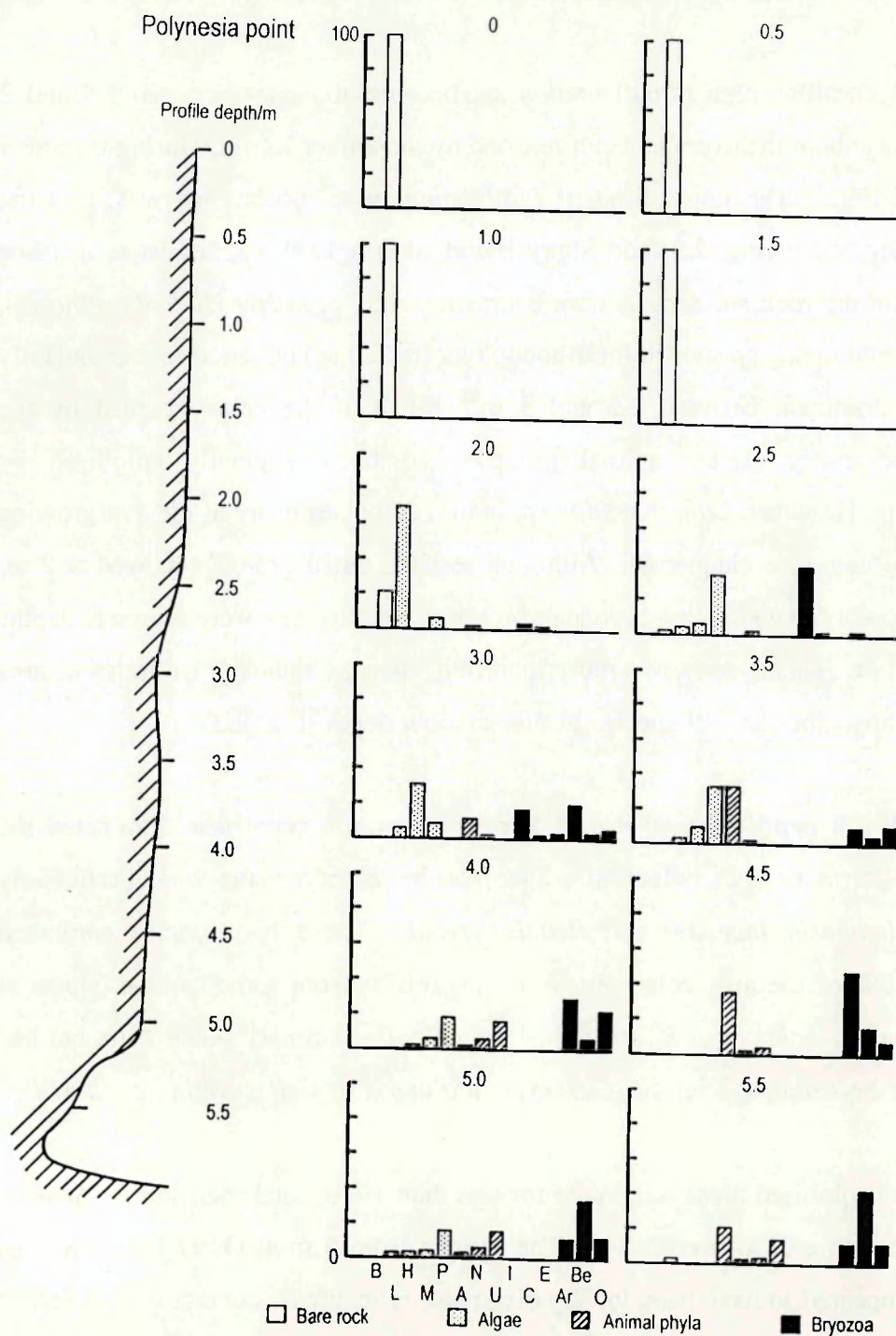


Figure 2.3c

The substratum profile with depths and associated histograms (scaled 0 to 100% cover) of transect at Polynesia Point. Zero depth datum corresponds approximately to mean low-water level. (T_{axa} = B bare rock; L, (probably) *Lithothamnion* sp.; H (probably) *Hildenbrandia* sp.; M, macroalgae; P = Porifera; A, Annelida; N, Cnidaria; U, Urochordata and other minor colonising phyla; bryozoans = I, *Inversiula nutrix*; C, *Celleporella bougainvillei*; E, *Escharoides tridens*; Ar, *Arachnopusia inchoata*; B, *Beania erecta*; O, other encrusting species)



predominantly echinoderms, molluscs, pycnogonids, isopods and a few species of fish, generally occurred in the areas of higher community development (and therefore probably areas of greater food abundance and frequency of shelter). Brachiopods, entoprocts and ascidians occupied little primary space at these sites, and so for convenience, were grouped together (data are summed into one bar for presentation; 'U' representing Urochordata (ascidians) and other minor encrusting phyla, in Fig. 2.3a,b & c).

The pink coralline alga *Lithothamnion* sp. became abundant between 1.5 and 2 metres, which was about the average depth reached by the winter ice foot during the study years 1991 and 1992. The upper limit of *Lithothamnion* sp. occurrence was, at some locations of Outer Island (Fig. 2.2) and Signy Island, strikingly sharp, almost as if a line had been ruled on the rock surface. A dark encrusting alga, probably *Hildenbrandia* sp., and various non encrusting species of the Rhodophyta (red algae) occurred less abundantly but were more dominant between 2.5 and 3 m. Much of the area occupied by the macroalgae (and many of the animal groups) had been originally colonised by *Lithothamnion* sp. However, *Lithothamnion* sp. in turn colonises many of the overgrowing organisms as epibiota (see chapter 6). Although sessile animal groups occurred at 2 m, with the exception of the encrusting bryozoan *Inversiula nutrix*, they were scarce at depths shallower than 3 m. This species was more than four times as abundant (in terms of area colonised) than any other animal species at this shallow depth (Fig. 2.3).

In samples at depths deeper than 3.5 m, sponges and bryozoans dominated the communities in terms of area colonised. Two species of bryozoans were particularly abundant: *Arachnopusia inchoata* and *Beania erecta*. These two species combined accounted for 80% of the area colonised by all organisms from some sample depths at these sites. Often *A. inchoata* or *B. erecta* had not colonised primary substratum, but had overgrown other bryozoan species such as *Inversiula nutrix* or *Celleporella bougainvillei*.

Bare or uncolonised areas accounted for less than 1% of total rock surface areas at depths of 4 m or more at all three sites. The sample from 5 m at Outer Island was an exception, but appeared to have been locally disturbed, probably by contact with ice (such

as drifting brash or iceberg remnants). Similar areas in this locality, at the same depth and profile, beside those on the sample transect, seemed to have a more developed benthos. Direct evidence of recent disturbance by ice included partly overgrown damaged remnants of bryozoan colonies. The community compositions of these sites also suggest recent recolonisation: the bryozoan species *Inversiula nutrix* and *Celleporella bougainvillei*, otherwise only common between 2 and 3 m, were abundant, and *Arachnopusia inchoata*, otherwise abundant in each 4 m or deeper sample at each site, was absent. This suggests a community in the early successional stages dominated by rapid colonisers (the bryozoans *I. nutrix* and *C. bougainvillei*), following the impact of ice.

Sponges overgrew bryozoans on 88.4% of the 232 recorded meetings of their respective growing edges, and ascidians overgrew bryozoans on 95.3% of 86 meetings. Only 11 interactions between sponges and ascidians were observed, and ascidians overgrew sponges on 9 (82%) of these occasions. Both sponges and ascidians were thus generally dominant in overgrowth interactions with bryozoans, and there is some suggestion that ascidians are dominant over sponges, although there are too few data to support a definite conclusion on this latter comparison.

Discussion

Sessile elements of the benthos were absent from the intertidal zone of the study areas and the few vagile or errant elements occurring were temporary itinerant summer visitors. A number of taxa, including representatives of sessile suspension feeding phyla such as the Bryozoa, did occur infrequently within the intertidal (chapter 4). So, as also found at the Fildes Peninsula (Rauschert 1986), limited intertidal faunas may occur in certain locations within Antarctica. At 2 m depth and below, coralline and macro algae became abundant. Fauna only became abundant at 4 m and deeper, as found by Rauschert (1991) at King George Island (Antarctic Peninsula). Zonation effects caused by disturbance may, however, reach deeper than this (see chapter 3). The data shown in figures 2.3a, b and c indicate that three broad zones may be identified:

- 1) 0 - 1.5 m, characterised by bare rock and winter ice foot formation.
- 2) 2 - 3.5 m, characterised by various types of coralline and macroalgae, and a faunal community in early development: characteristic bryozoan species include *Celleporella bougainvillei*, *Inversiula nutrix* and *Escharoides tridens*.
- 3) 4 - 5.5 m, characterised largely by bryozoans but also, to a lesser extent sponges. Characteristic bryozoan species; *Arachnopusia inchoata* and *Beania erecta*.

A number of empirical methods have been developed for diversity studies (reviewed in Magurran 1988), but these were largely inappropriate for this study because of the mixed level of taxonomic resolution. The data set may be analysed empirically for species richness (total numbers of species) by restriction to those taxa which were identified to species, which in this study was solely the Bryozoa. Analysis of variance indicated a significant increase in the number of species with depth in all three transects ($P < 0.05$). The number of phyla also increased significantly with depth. As the sampling procedure was designed as a quantitative approach to distribution of taxa along transects, rather than a diversity study, the information obtained precludes calculation of formal diversity indices.

The Bryozoa, as well as being a dominant component in the communities of epibiota at these depths and locations (chapters 6 & 7 of this thesis, Barnes 1994, Barnes & Clarke 1995b), occupied more space than other taxa at all three sites surveyed. The results, when summed over all sites, show that different species of Bryozoa exhibited maxima in area occupation at different depths (Figs 2.3a, b & c). *Inversiula nutrix* peaked at 2.5 m, *Escharoides tridens* at 3 m, an assemblage of minor space occupying species (e.g. *Ellisina antarctica*) at 4 m, *Arachnopusia inchoata* at 4.5 m and *Beania erecta* at 5.5 m. Those species which peaked at the deeper end of the sequence (for example *B. erecta*) had often overgrown the original colonisers, which were usually the same species occurring at the shallower end of the sequence. At similar locations where the ice foot was greater in duration and probably thickness, such as found in sheltered coves (e.g., Porny Rock, Barnes

& Clarke 1994), community development only reached the level characterised by zone 2: the bryozoans *I. nutrix* and *E. tridens* dominated the community from 2 m to the base of the vertical face at 4.5 m, and *B. erecta* was completely absent.

For geographical areas outside the polar regions there is a substantial literature on sublittoral hard substratum community dynamics. Bryozoans have generally been found to be poor overgrowth competitors against other modular organisms (Stebbing 1973, Osman 1977, Buss 1979, Keough 1984). In the present study sponges and ascidians, despite occupying only small areas, similarly appeared to be dominant overgrowth competitors over bryozoans (overgrowing bryozoans in 88.4% and 95.3% of meetings respectively). The relatively low area occupied by the competitively more dominant taxa thus indicated that the communities were in early successional stages. If the bryozoans have a comparatively high larval production rate, such that they arrive early in the faunal colonisation succession of recently available substratum and/or have a fast rate of growth, continual disturbance by factors such as ice scour, would result in an assemblage dominated by bryozoans.

Sessile suspension feeders, in particular bryozoans, sponges and ascidians are described as dominating many of the benthic communities reported from Antarctic shelf locations (Winston 1983, Voß 1988, Winston & Heimberg 1988, Galéron *et al.* 1992). The relative abundance of the Bryozoa, compared with other sessile suspension feeding phyla, in such deeper water studies, is usually much reduced from the dominance found at shallow depths in this study (see chapter 3).

Factors affecting community development and composition

The influence of disturbance on community development and consequently species diversity, has been described for a variety of marine environments, in particular the intertidal of temperate rocky shores. Intermediate levels of disturbance, either by physical or biological forces, have been found to be associated with high levels of species diversity over a wide range of depths from the intertidal (Paine & Vadas 1969, Lubchenco 1978) through the sublittoral (Ayling 1981, Sebens 1985) to the deep sea (Dayton & Hessler

1972) and in habitats ranging from coral reefs to rain forests (Connell 1978). An important role for disturbance (here by ice) is suggested by the present study for the Antarctic sublittoral.

In this study, physical disturbance by ice occurred throughout the year at the shallowest region of the transects (zone 1), this disturbance included the development and persistence of the ice foot during winter, and intermittent scouring from drifting brash ice during summer. In open water periods there is additional disturbance from wave and current action, as well as occasional exposure to air during extreme low water spring tides. Anchor ice, which has been described as a major influence on sublittoral communities in the high Antarctic (see Dayton *et al.* 1970), is relatively rare and thus probably had little influence at Signy Island. Community development in zone 1 is thus most restricted by winter disturbance (ice foot formation). The stabilising effect of surface sea-ice means that, in contrast, winter is the period of minimum disturbance for zones 2, 3 and the deeper sublittoral. In zones 2 and 3 (2 - 5.5 m depth) there is nevertheless some summer scouring by ice which restricts community development such that the more competitively dominant sponges and ascidians occupied a smaller proportion of the community than the apparently more rapidly colonising bryozoans. Depth thus influences community composition on upper sublittoral hard substrata at Signy Island through its relationship with the frequency and/or intensity of ice impact.

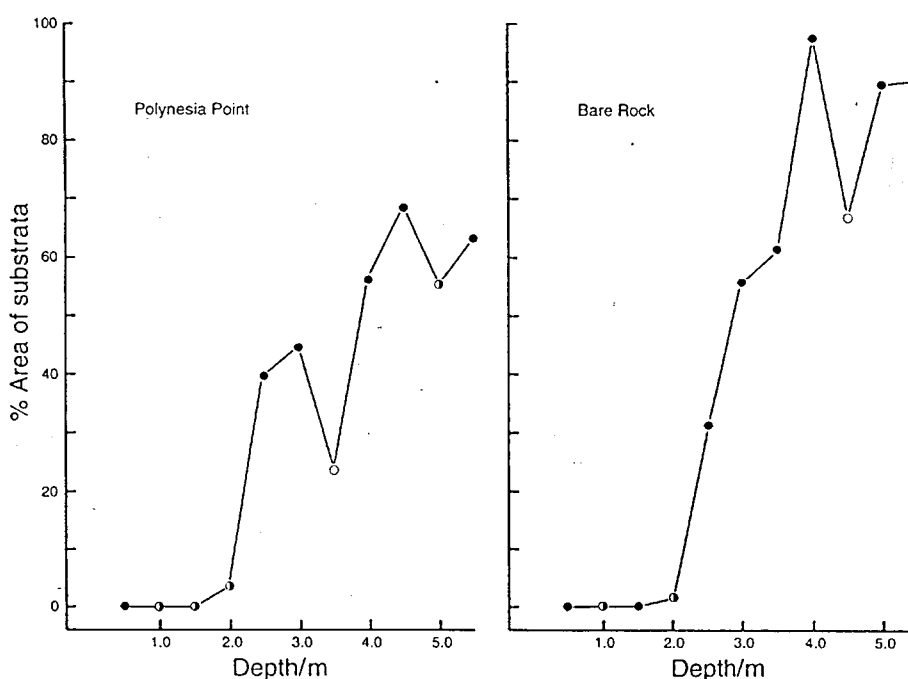
The similarities between the findings of this study and that by Dayton (1971) on the Washington coast of the U.S.A., suggest a parallel between the physical disturbance of intertidal communities by drifting ice in the maritime Antarctic and drifting logs along the Pacific coast. In each instance monopolization by a few species is prevented and competitive dominants may rarely occupy more than relatively small areas of substratum. Clearly the communities in both areas are governed to a great extent by disturbance factors.

Another factor, besides depth and disturbance, which may have a large influence on benthic community composition is substratum profile (Noble *et al.* 1976, Logan *et al.* 1983, 1984, Kirkwood & Burton 1988, De Kluijver 1993, Barnes 1995a; also see chapter

3). Although the depth profiles at the three sites were approximately vertical, slight variations did occur and these may be of importance to the community composition especially at the deeper end of the spectrum. Most of the profile of both Bare Rock and Polynesia Point was overhang, but at one sample point at each site the profile incline shallowed (illustrated by open circle in Figure 2.4). The total area occupied by bryozoans seemed to be lower at locations where the profile inclined than might be predicted by depth (mean decline of 26.8%, SE 16.8, $t_{18}=2.45$, $P < 0.05$). In both cases the reduction of area occupied by bryozoans occurred simultaneously with an increase in the area occupied by sponges. The total area of substratum colonised remained virtually unchanged, however.

Figure 2.4

Percentage area of substratum occupied by bryozoans as a function of depth, at Bare Rock and Polynesia Point, substratum orientations are ● overhang; ○ vertical; ○ inclined. Zero depth datum refers to mean low-water level.⁵⁹



This chapter has dealt specifically with the communities growing on vertical hard substrata. However, three basic types of substratum occur locally: soft sediment, mixed pebbles and vertical rock. Each has a completely different community composition. Substratum type is, therefore, overall the most important factor influencing community

composition in the sublittoral at Signy Island, as has also been found in the Davis Sea (Kirkwood & Burton 1988). Between 2 and 5.5 m, rock faces may develop complex communities covering 100% of the substratum, compared with more impoverished communities on the sediment or mixed pebbles. Within the framework of a given substratum, however, ice effects were the dominant factor affecting the intertidal and shallow sublittoral (0-2 m depth) community structure and is the major factor inducing vertical zonation. Disturbance by ice also seems to be important in limiting community development within the 2 - 5.5 m zone. Whilst ice effects decrease with depth, the profile becomes more important, so ice, profile and depth are all interlinked. Community development on hard substrata in shallow water at Signy Island is dictated by a number of environmental factors, which change in relative importance with profile.

Sublittoral epifaunal communities: Below the ice foot zone

Introduction

Dense and sometimes taxonomically rich communities of Antarctic marine benthic herbivores have now been described from shelf locations around the Antarctic continent (Belyaev & Uschakov 1957, Tressler 1964, Propp 1970, Gruzov 1977, Voß 1988, Galéron *et al.* 1992). In the sublittoral the distribution of such communities has been found to be particularly dependent on aspects of both substratum (Kirkwood & Burton 1988, reviewed in Arntz *et al.* 1994) and ice (Dayton *et al.* 1970, 1974). At Signy Island in the maritime Antarctic, despite the short duration and unpredictable intensity of primary production, and the typically long period of annual sea-ice cover (Whitaker 1982, Clarke *et al.* 1988), the benthos is diverse and abundant even in the shallow sublittoral (White & Robins 1972, Barnes 1995a,b).

Chapter 2 described the composition and community dynamics of the hard substratum benthos in the infralittoral ($\approx 0 - 15$ m) at Signy Island, in addition to major structural influences such as the formation and persistence of the seasonal ice foot. This chapter examines the distribution, abundance and possible influences on hard substratum benthic communities from the ice foot zone, at sea level, to 40/50 metres depth. Particular attention was paid to bryozoans and their ecology in comparison with other colonising phyla. The main aims of the study were to determine the variation with depth of the percentage cover of substratum, the taxonomic composition of the community and ecological aspects of the bryozoan component (such as growth morphologies).

Materials and methods

Study site and species

The transect component of this study was undertaken at Powell Rock and Outer Island,

close to the British Antarctic Survey research station at Signy Island, South Orkney Islands in the maritime Antarctic. SCUBA observations were also made over a similar depth range of at number of other locations within Borge Bay. Specimens from 50-290 m were obtained from bottom trawls in Outer Borge Bay, between Signy and Coronation Islands.

Limitations of underwater time, particularly at deeper parts of the SCUBA transect (0-40 m), dictated the use of photographic techniques. This in turn limited the taxonomic resolution of the study. To facilitate interpretation of these transects, and partly due to taxonomic complexity, algae were placed into three groups: macroalgae, the coralline alga *Lithothamnion* and the similar *Hildenbrandia* (Table 3.1). Five animal phyla were recorded: sponges, cnidarians, urochordates (ascidians), brachiopods and bryozoans. The latter phylum, being particularly abundant, was subdivided into four morphological groups: encrusting, massive encrusting/ foliaceous, erect flexible and erect rigid (Table 3.2). The trawled specimens were available for detailed taxonomic study and various species of bryozoans are listed under these different morphological groups in the trawling results; the statistical comparisons were made between these morphological groups and not the individual species. Some animal taxa were present but unrecorded; these included the annelids and entoprocts which occupied very small areas of substratum.

Transect method and analysis

The field work and analysis took place over the austral winter of 1991. At each station, photographic samples were taken every 5 m along transect lines running from the sea ice to 40 m depth. The Outer Island 40 m transect was at the south end of the island; this is a different location from the 5 m transect at Outer Island described in the previous chapter, hence the difference in profile. Five photographs were taken, each covering an area of 0.5m², at every 5 m increment, using an underwater camera (as described in chapter 2). Colour reversal film, developed on site, was projected onto a regular grid of 7700 points. The amount of area occupied by the base of each group was divided into the total area of the photograph to give the percentage area covered (see chapter 2). Mean values for each taxonomic group were calculated from the five replicates at each depth. Profiles of each

site were also recorded.

Trawl method and analysis

Specimens were collected and sorted from 28 trawls, at depths ranging from 50 m to 290 m, during the austral summer of 1991/92. An Agassiz benthic trawl was towed for bottom durations of 15 minutes at each location. A combination of echosounder and hydrographic charts was used to ensure that each sample came from a narrow depth range (within 10 m of the nominal depth). This aspect of the study was concerned solely with bryozoans. Bryozoan specimens were identified on sorting, or by Dr P.J. Hayward at the University of Wales (Swansea). Species were recorded as either abundant if they were found in more than two trawls from any one depth or merely present if found in two or fewer.

Table 3.1

Taxa of organisms occurring in communities surveyed by SCUBA transects at Powell Rock and Outer Island, Signy Island, Antarctica (NR = not recorded)

Phyla present	Designation	Comments
Phaeophyta, Rhodophyta	'Macroalgae'	Macroalgae grouped because of taxonomic complexity
Rhodophyta	Genera <i>Lithothamnion</i> and <i>Hildenbrandia</i>	Separated from macroalgae because of growth form
Porifera	phylum Porifera	
Cnidaria	phylum Cnidaria	
Annelida	NR	insignificant area occupied
Mollusca	NR	mobile fauna
Entoprocta	NR	insignificant area occupied
Brachiopoda	phylum Brachiopoda	
Bryozoa	morphological groups	listed in Table 2
Echinodermata	NR	mobile fauna
Chordata	ascidians	

Table 3.2

Bryozoans, grouped according to colony growth form, recorded between Signy Island and Coronation Island along transects (0 to 45 metres using SCUBA) and by trawls (50 to 290 metres).

Growth form of bryozoans	Transect (0-45m)	Trawl (50-290 m)
Encrusting	+	
Encrusting massive	+	+
Erect flexible	+	+
Erect rigid		+

Results

At both transect locations the substratum profile was a shallow slope down to about 15 m, with one small vertical face at each site (Fig. 3.1a & 3.1b). The rock face then steepened to 25 m at Powell Rock and 35 m at Outer Island. Below this depth the substratum at both sites was characterised by shallow sloping rock rubble, until about 37 m whereafter it comprised soft sediment with occasional rock outcrops.

The taxa recorded on the SCUBA transects are listed in Table 3.1. Coralline algae (mostly *Lithothamnion* sp.) dominated the shallow sloping shallow water component of both transects. Another coralline alga (probably *Hildenbrandia* sp.) became more abundant at about 15 m, likewise macroalgae of the genera *Desmarestia*, *Phylogigas*, *Delisia* and *Iridia*, such that algae in general were the major occupier of space almost throughout the transects. At the deep end of the transect (35 m and deeper), the macroalgae were the largest occupier of space, and at 40 m macroalgae were the only algal group present. Animal phyla generally became abundant at about 15 m, although they were also locally abundant at shallower depths where vertical faces occurred. Of these animal taxa bryozoans and sponges were by far the occupiers of most space, although representatives of the ascidians, cnidarians and brachiopods were also very common in places. Some animal phyla such as annelids and entoprocts were common but occupied relatively small areas. Other phyla, which were not sessile or encrusting, such as the echinoderms, were

Figure 3.1a

Substratum profile of the transect at Powell Rock, with percent substratum cover by colonising benthos represented as pie charts (substratum types: hatching rock face; circles rock/pebble rubble; dots sediment) Pie chart data presented as mean of five samples of percentage area of substratum occupied. The section of each pie representing the bryozoa is shown exploded.

POWELL ROCK

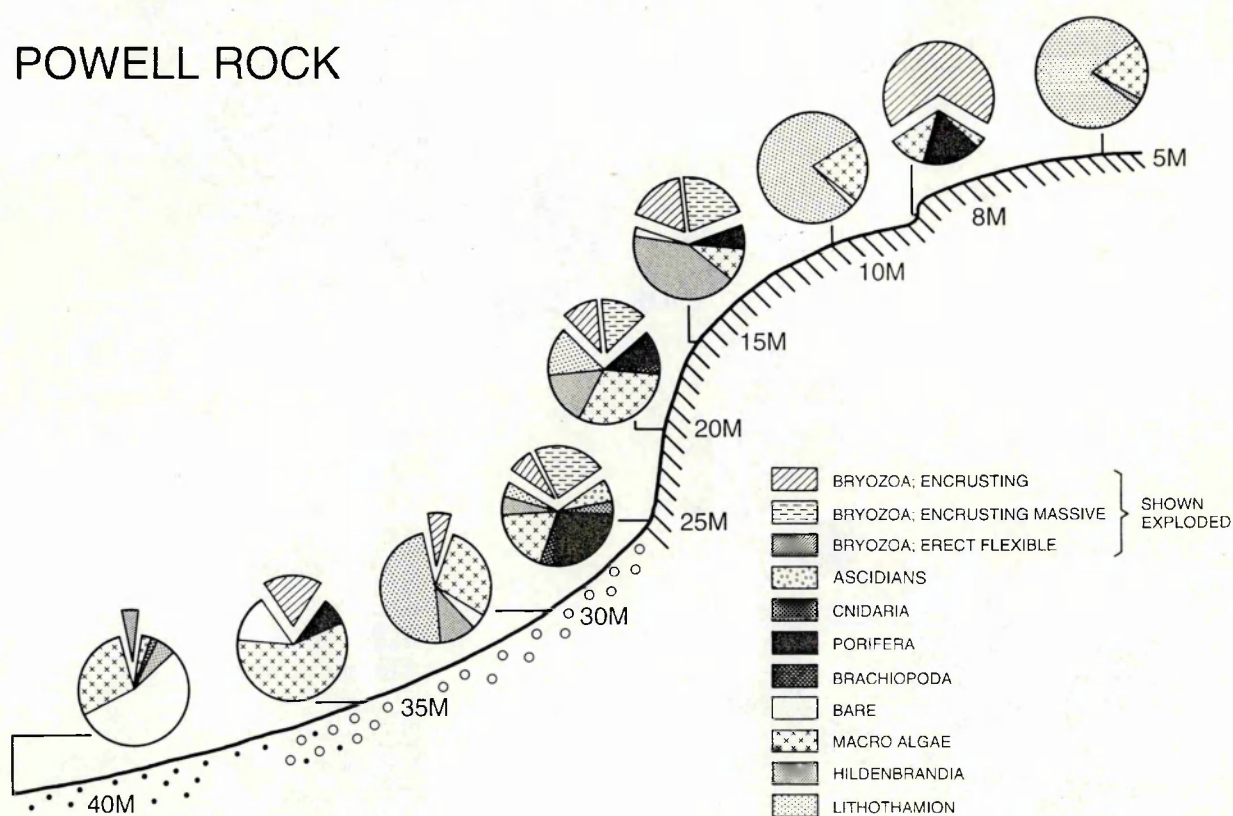
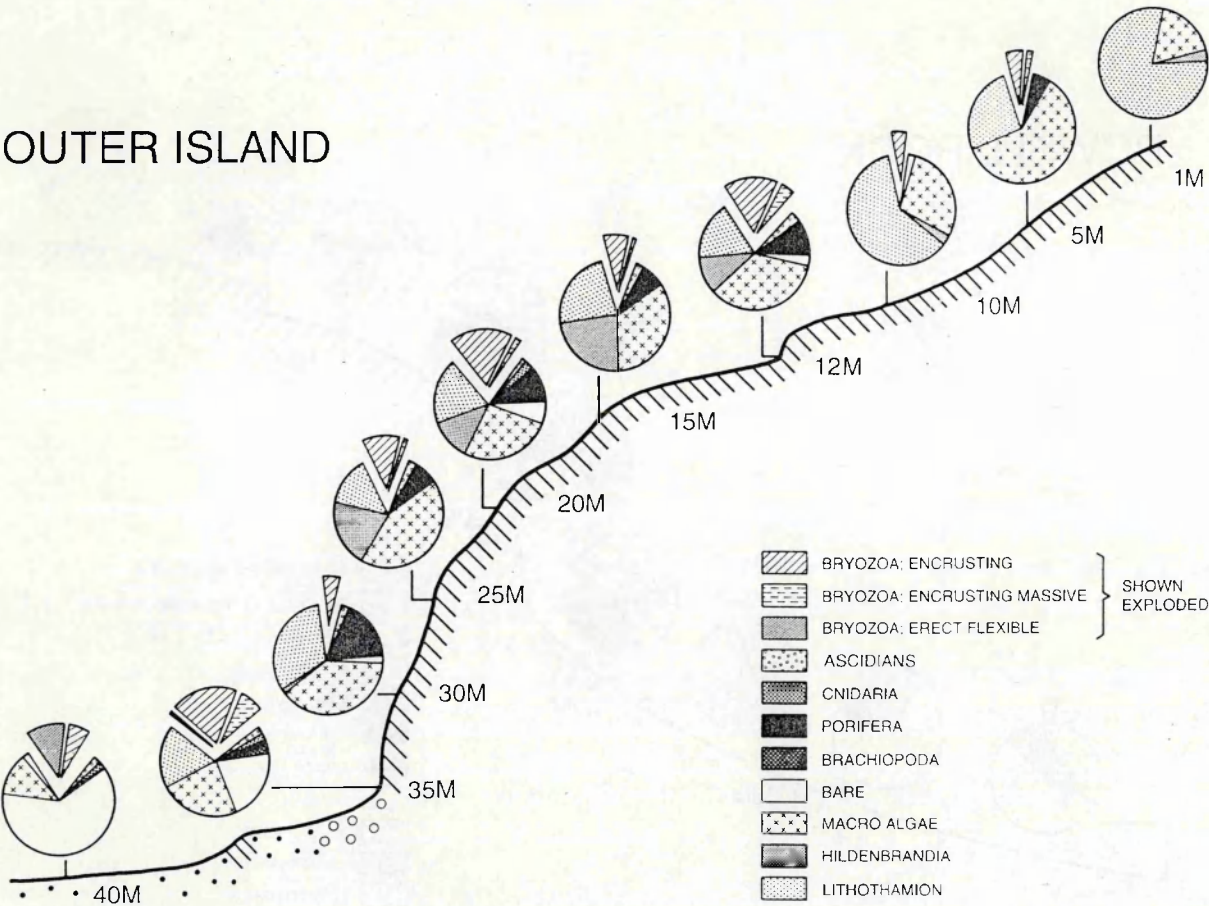


Figure 3.1b

Substratum profile of the transect at Outer Island, with percent substratum cover by colonising benthos represented as pie charts (substratum types: hatching rock face; circles rock/pebble rubble; dots sediment) Pie chart data presented as mean of five samples of percentage area of substratum occupied. The section of each pie representing the bryozoa is shown exploded.

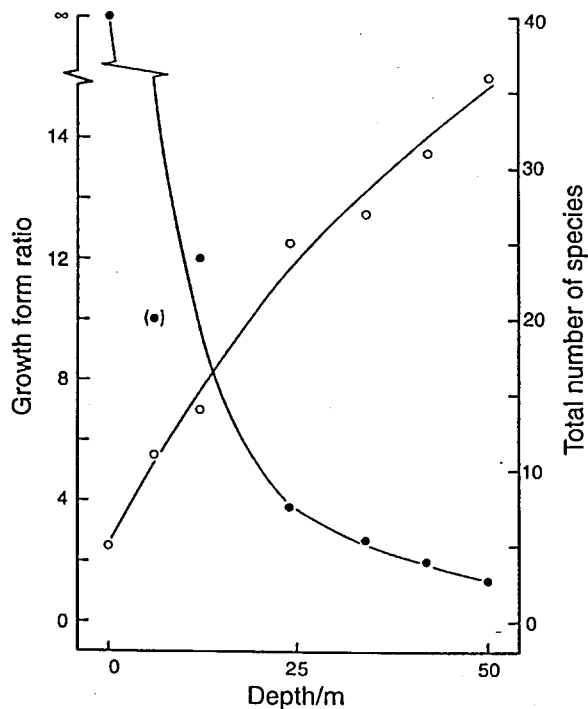


not recorded, despite being locally abundant on some transects. The amount of substratum devoid of surface colonisation increased dramatically at 35 m, to over half at 40 m.

Animal groups were the largest occupiers of space in only a few locations, and at these locations, bryozoans constituted the major proportion. The bryozoan component of the SCUBA transects were divided into 3 broad morphological groups: encrusting species dominated by *Beania erecta*, encrusting massive/ foliaceous species dominated by *Arachnopusia inchoata* and *Lageneschara lyrulata* (Calvet), and erect flexible species dominated by *Alloeflustra tenuis* (Kluge) and *Nematoflustra flagellata* (Waters). The encrusting group constituted an important proportion of the bryozoa from the shallowest locations at which the phylum occurred to 35 m. The encrusting massive group was much more abundant at Powell Rock than Outer Island, and at either site was found only on the steeper areas of rock face. In contrast, the erect flexible group was abundant only at 40 metres on the sediment substratum, where it was the largest occupier of space, not only of the bryozoan groups, but of all the animal phyla.

Figure 3.2

Ratio of encrusting and encrusting massive/ foliaceous to erect (flexible and rigid) cheilostome Bryozoa and number of species as a function of depth from 0 to 50 m. [● ratios of total numbers of species found at these depths at all study locations in Borge Bay; (●) single specimen of one erect species found from unusually shallow location; (○) total numbers of cheilostome species found at these depths at all study sites] Data points for 50 m depth were taken from trawl data.



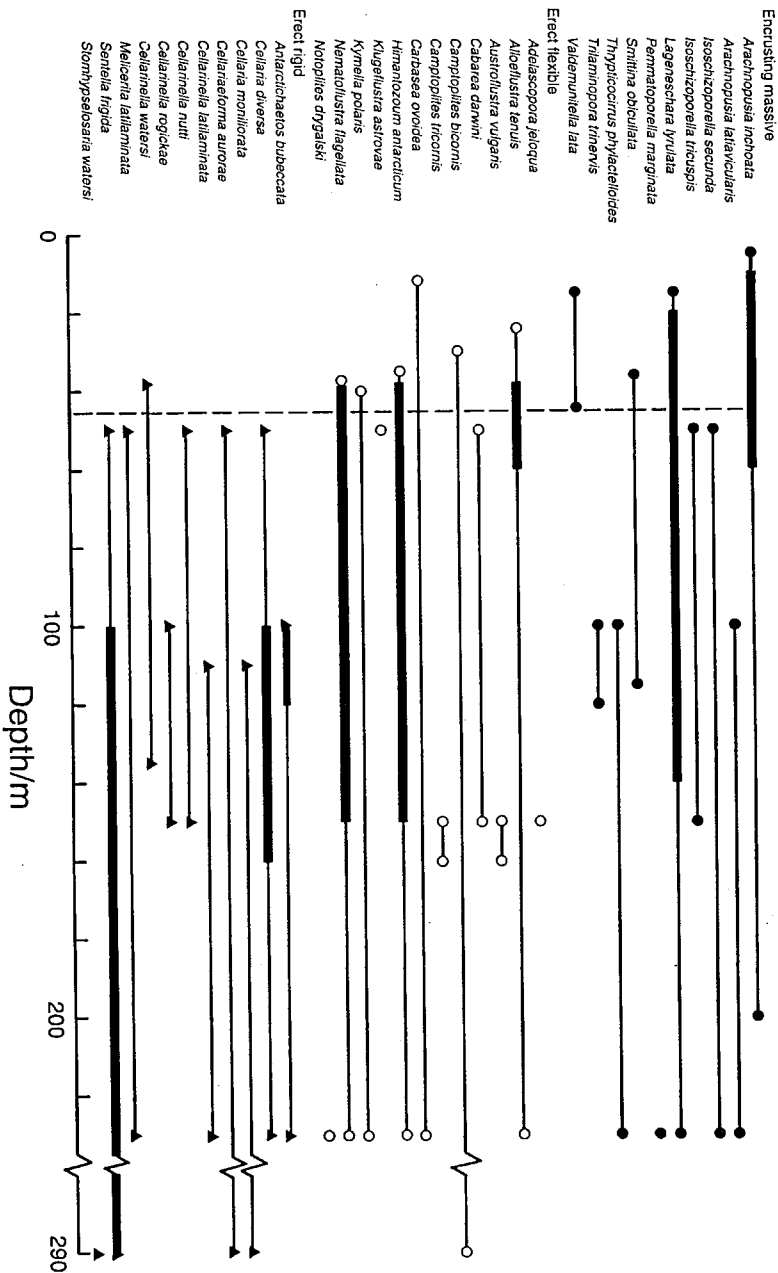
Variation of bryozoan morphology with depth

In both the SCUBA transects, the bryozoan morphology occurring shallowest was the encrusting form, followed with increasing depth by encrusting massive/ foliaceous and finally erect flexible forms. The ratio of encrusting (including encrusting massive/ foliaceous forms) to erect species was calculated from this study together with data collected from the parallel companion study (see chapter 2) and incidental SCUBA observations. This ratio showed a striking variation with depth (Fig. 3.2). The outlying point at 6 m depth was due to a single colony of an erect species. One species (*Arachnopusia inchoata*) changed classification between 12 and 24 m: it was a predominantly encrusting form in shallow water but an erect form in deeper locations.

Erect forms were abundant in the trawled material, whilst encrusting forms were virtually absent. This was partly a sampling artefact as trawling would have collected erect forms preferentially, although the trawled biota suggested that the substrata encountered were mostly soft sediments, where encrusting species would be rare. The 33 erect species found were grouped into three morphological categories; encrusting massive, erect flexible and erect rigid. The erect rigid forms were recorded from trawled material but not from the SCUBA transect (Table 3.2). Of these 33 species, 8 were classified as abundant (present >2 trawls at any depth), whilst 3 species were only recorded at one location. These trawl data have been combined with information obtained from SCUBA in the range 0 to 45 m, to provide an overall picture of bryozoan distribution (Fig. 3.3). There were no trawls spanning the depth range 230 to 290 m, although species found at both 230 and 290 m are joined by a continuous line. *Carbacea ovoidea* (Busk), shown occurring shallower than other erect flexible species, was represented by only a single colony shallower than 18 m.

Depth distributions of 33 erect cheilosstome species of Bryozoa from 0 to 290 m. Species grouped into three morphological forms (● encrusting massive; ○ erect flexible; ▲ erect rigid, filled bars abundant; lines merely present) Dashed line separates 0 to 45 m data from observations and collections using SCUBA and 50 to 290 m data from 28 discrete benthic trawls.

Figure 3.3



Discussion

Distribution and abundance of phyla from 0-40 metres

Benthos other than algae was scarce shallower than 12-15 m, although the degree of substratum colonised shallower than 12-15 m was approximately 99% (Fig. 3.1a & b). From 15-30 m a number of taxa were abundant and the colonisation level of the substratum remained high, though both number and abundance of taxa and the percentage of substratum occupied decreased rapidly to 40 m. Little is known of the zone immediately below 30 m in Antarctic waters (Arntz *et al.* 1994), as it is considered too deep for routine SCUBA diving, and too shallow for ship-based trawling work. Sponges and their predators were characteristic at this depth in those areas studied in McMurdo Sound (Dayton *et al.* 1974). Between 30 and 40 m in both SCUBA transects, and at other studied areas at this depth at Signy Island, the substratum changed from hard rock to predominantly soft sediment. Determination of zonation within this deeper region was not possible because of the difficulties of separating the effects of depth, profile and substratum.

Along the course of the transect, the orientation of the hard substratum profile of both Powell Rock and Outer Island changed considerably. Coralline algae tended to dominate upward facing rock, particularly in the shallow locations, but the presence of a steeper or vertical slope, as seen at 12 metres at Outer Island and 8 m at Powell Rock, resulted in a shift in balance from coralline algae to animal taxa. The colonising biota at the 1 and 5 m locations of the two transects were very different from those of the transects at Signy Island which covered this depth range with similar substrata types but with vertical profiles (Barnes 1995a; chapter 2). Small changes in profile produced large changes in taxonomic composition and abundance, within the 5.5 m range covered by the other study. Although there were some effects of profile on taxonomic composition and abundance below 15 m depth in this study, these were small: relatively large variations in profile produced smaller changes in biota. This would suggest that the influence of profile on epifaunal composition is at its greatest in the shallower locations studied. Profile affects both the amount of light reaching the substratum and the frequency and degree of damage

by floating ice. Both of these factors will be more pronounced at shallow locations, as ambient light and the frequency of ice scour decrease with depth. As a result (light-dependent) algae dominate the shallow upward facing substratum and light-independent animal groups dominate the shallow vertical substratum.

Major changes in community composition with substratum orientation are well known from non polar latitudes, particularly from a number of recent rocky shallow subtidal studies on the coast of New England (Steneck 1978, 1986, Garwood *et al.* 1985, Sebens 1986a,b, Ojeda & Dearborn 1989). Such studies have similarly documented domination by coralline algae on inclined (and horizontal) shallow rock and by encrusting fauna on vertical or overhanging rock. There are fewer studies of hard substratum communities in deeper water (or what has been termed the circalittoral; see Logan *et al.* 1984, Logan 1988) below the infralittoral (0-14 m). Circalittoral communities of the Bay of Fundy are described by Logan (1988) as being dominated by encrusting fauna irrespective of rock orientation.

The influence of depth may be separated from that of profile by comparing the communities at locations of different depths but similar profiles: for example the vertical hard substratum at the Outer Island and Powell Rock 25 m sites with those at 8 m at Powell rock and the three 5.5 m surveys (see chapter 2). Whilst the two 25 m locations were characterised by a number of abundant phyla, the shallow locations were dominated by bryozoans. Observations of the overgrowth hierarchy during this study and others elsewhere (see chapter 2) have found that bryozoans were overgrown by most other animal phyla on contact. Perhaps the higher disturbance frequency by ice at 5-8 m restricts community development to a greater degree than at 25 m. Large areas of substratum at 15-25 m were occupied by competitively weak taxa (taxa that were usually overgrown at contact with other taxa). This suggested that the disturbance frequency of the 15-25 m study sites was instrumental in maintaining the high level of faunal diversity, as has been suggested for deep sea benthos (Dayton & Hessler 1972), and proposed as a general hypothesis of diversity regulation (Grime 1973, Connell 1978, Huston 1979).

Zonation with depth was also noted on other substrata, such as sediment. At several locations within Borge Bay the substratum was dominated by soft sediment from 4-48 m, but the surface was virtually uncolonised by superficial fauna at depths shallower than 35 m (although a number of burrowing species are present beneath the substratum surface). Substratum type, therefore, had the largest affect on taxonomic composition and abundance of colonising biota, but for a given substratum type, depth and profile were important factors, as found in macrobenthos studies of the Davis Sea (Kirkwood & Burton 1988).

Distribution and abundance of bryozoans 0-50 m

At nearly all the locations in this study, irrespective of substratum, depth and profile, bryozoans were the largest occupiers of space of all the animal phyla. Such levels of abundance or area dominance by bryozoans have rarely been described from the sublittoral of other latitudes with the exception of cryptic habitats such as caves (Harmelin 1985, 1986), the undersurface of coral heads (Jackson 1979) and a few unusual localities in New Zealand (Saxton 1980a,b, Bradstock & Gordon 1983). The proportion of area occupied, the morphological group, and the species dominating within bryozoans, all changed with substratum type, profile and depth. *Arachnopusia inchoata* was abundant in encrusting form in shallow water and as a large foliaceous form in deeper water. Mechanical damage from wave and current action may have been largely responsible for a shift in surviving morphology with depth rather than an actual shift of growth morphology with depth.

At certain locations, encrusting species occurred as shallow as the intertidal (chapter 4), encrusting massive species were common on hard substrata at 15 m and deeper, and erect species became abundant at 35 m and deeper. At Borge Bay, Signy Island, the ratio of encrusting to erect species approached unity by 50 m (Fig. 3.2). The number of species at 50 m was 36 compared with just 5 recorded in the intertidal zone. Much of this increase in the number of species with depth reflects the increasing numbers of erect species. Thus, even where bryozoans were abundant at 40 m and deeper, the coverage of substratum surface was small compared with those on hard substrata.

Distribution and abundance of erect bryozoans from 0-290 metres

The separation of the erect cheilostome bryozoan species into morphological groups (Fig. 3) is very useful for broad comparisons, although conclusions must be treated with an element of caution because of:

- 1) Sampling technique difference: collection using SCUBA < 50 m and trawls 50-290 m.
- 2) Trawling bias: not all species are equally likely to be represented in collections.

Many of the erect species, of all morphologies, occurred over much of the depth range encompassed by this study (Fig. 3.3). These results suggest that the encrusting massive/ foliaceous forms occurred and became abundant at the shallower depths, but were scarcer at the deeper locations than the erect flexible forms. The latter, as a group, had a similar distribution pattern but were abundant at shallower depths than were the rigid erect species. The erect form of growth, whilst possibly conveying advantages over encrusting forms in feeding, competition and substratum utilisation (Cheetham 1971, Jackson 1979, Grosberg 1981) encounter the problem of resistance to water flow (reviewed in McKinney & Jackson 1991). Most erect bryozoan species occurring in environments likely to experience high water flow rates are flexibly erect, although this study showed some encrusting massive species occurring in shallower locations. This is because these species (e.g., *Arachnopusia inchoata*) grow mostly in the encrusting form when shallower than 15 m. Only one small community of a single rigid erect species, *Cellarinella watersi* Calvet, was found shallower than 50 m, but rigid erect forms are abundant in deeper Antarctic locations (Winston 1983).

Conclusions

Dense benthic communities occur in very shallow water at Signy Island and at depths greater than 15 m these communities can be taxonomically rich. The overall patterns of distribution of benthos described in this study are a similar and form a continuum with the descriptions of the intertidal and upper sublittoral benthos in chapter 2. Similar

conclusions were also drawn on environmental influences on these patterns: the seasonal formation of an ice foot prevents virtually all colonisation within the intertidal, but immediately below this the change in frequency of disturbance with depth and profile probably accounts for most of the variation in hard substratum communities.

The principal faunal component, in terms of area colonised, at this depth range is bryozoans. Although Antarctic bryozoans are overgrown by most other faunal elements, the frequency of disturbance (largely by ice) and recolonisation, results in the faster colonising bryozoans occupying the most area. The dominant morphologies of bryozoans change with increasing depth (which at the study locations was also linked with a change from hard to soft substratum) from predominantly encrusting forms through a variety of erect morphologies. There is a considerable degree of overlap within these forms.

These studies have shown bryozoans to be important colonisers of hard substrata, particularly those with moderate frequencies of disturbance. Amongst natural hard substrata, however, rock faces are the most stable and suffer the least disturbance. Thus to study bryozoan community ecology in detail, more unstable substratum (boulders and pebbles) must be examined.

Colonisation and competition on unstable substrata : outcomes, influences and implications

Introduction

Competition, predation and disturbance have been shown to be important influences on the structure and diversity of hard substratum communities (Dayton 1971, Paine 1974, Osman 1977, Russ 1980) and encrusting sublittoral assemblages have become a key area for the study of the mechanisms involved in competition for space and food. The relative degrees of overgrowth by and of each species, in competition, may form either a hierarchical sequence (e.g., Connell 1961a,b, Stebbing 1973) or a network without complete dominance (Buss & Jackson 1979, Buss 1980, Liddell & Brett 1982, Sebens 1986). Networks are thought to be prevalent in assemblages with greatest variety of form such as those involving many phyla (Jackson 1979a) or bryozoans (Quinn 1982). This is because the outcome of overgrowth interactions vary with many factors. The presence of competitive networks (termed intransivity) has been shown to be responsible for maintenance of taxonomic diversity in some environments where the influences of predation or physical disturbance are minor (Jackson & Buss 1975, Buss & Jackson 1979). Disturbance, particularly that mediated by icebergs (Richardson & Hedgepeth 1977, Peck & Bullough 1993), anchor ice (Dayton *et al.* 1970, 1974, Zamorano 1983) and the presence of an ice foot (Kotlyakov & Smolyarova 1990, Barnes 1995a), is a major factor within the Antarctic sublittoral and is likely to be a major influence on community dynamics at Signy Island.

Field studies using artificial substrata have shown cheilostome bryozoans and polychaetes to be dominant or important early constituents of encrusting marine communities in the sublittoral at low (temperate/tropical) latitudes (Jackson 1979a, Rubin 1985, Todd & Turner 1989, Turner & Todd 1994). This dominance is particularly pronounced in the few similar studies that have been undertaken at high latitudes (Moyano 1984, Lopez Gappa 1989, also see chapter 5). The habitats on unstable natural substrata, such as small boulders and pebbles, have been found to also support communities in which bryozoans are often dominant (Osman 1977, Rubin 1982). Although some broadscale

studies of shallow water rock faces in Antarctica have revealed large benthic communities (e.g., White & Robins 1972, Gruzov 1977, Kirkwood & Burton 1988), this thesis and associated papers represent the only examination to date of marine community dynamics on smaller scale, unstable, natural substrata, in Antarctica.

This chapter describes community composition and competition, with emphasis on bryozoans, on natural substrata from several sites at Signy Island, Antarctica. The degree of colonisation and community change (in composition and location) was examined with respect to substratum surface area and depth and the outcomes of intra and interspecific competitive encounters amongst assemblages of cheilostomatid bryozoans.

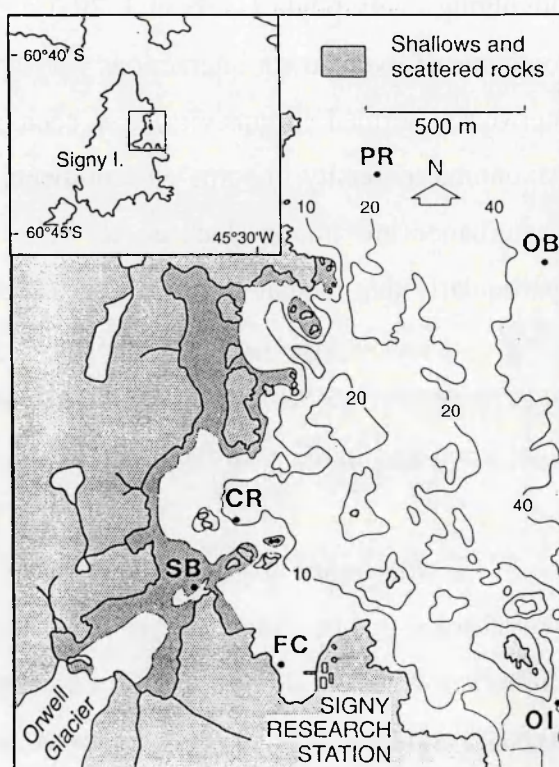
Materials and methods

Study site and species

Rocks were collected at six locations from Borge Bay, at Signy Island (Figure 4.1). These sites differed with respect to depth (and consequently disturbance) and to a minor extent, duration of ice cover. The seasonal cycle of temperature, ice cover and chlorophyll standing crop experienced at Cam Rock (12 m), Powell Rock (24 m), Owens Bank (34 m) and Outer Island (42 m) are approximately similar, and are described in Clarke *et al.* (1988) and Leakey *et al.* (1994). The duration of ice cover and exposure to ice related disturbance, such as scour from icebergs (Barnes & Clarke 1994), was greater in Factory Cove (6 m) than at the deeper sites, and greater still at Shallow Bay (intertidal).

Figure 4.1

Map of Signy Island showing collection sites (●) in Borge Bay. Site labels are, SB: Shallow Bay, FC: Factory Cove, CR: Cam Rock, PR: Powell Rock, OB: Owens Bank, OI: Outer Island.



The temperature and salinity regime at the intertidal site, Shallow Bay, differed substantially from the deeper sites. Daily summer variations in low water pools at Shallow Bay was found to range from -0.5° to $+10.7^{\circ}$ in temperature, and from 8 ppt to 26ppt salinity. This daily variation was in excess of four times the annual variation generally experienced nearby in Borge Bay (Clarke *et al.* 1988). The physical dimensions of each site and the substratum present were approximately similar, comprising of a rock-pebble mix with surrounding mud, although the cover of sediment on rocks at the 42 m site was greater than on shallower rocks.

Between 150 and 200 rocks were collected at random from an area approximately 2 m^2 at each of six sampling locations described above. All bryozoans present on each rock were identified to species and the number of bryozoan species and colonies of each species were counted and recorded for each rock. All other organisms present were identified to phyla. The total area colonised by all organisms, and the overall surface area of each rock was measured using a fine net marked as a grid of square centimetres. The colonising organisms were measured using the same method and ranked for each rock according to area occupied. The orientation of colonies (top or bottom of the rock) was recorded, using the presence of coralline algae to denote the top surface. The presence of coralline algae was also used as a relative indication of the turnover rate of rocks; the rocks were classed into size groups for each depth, and the proportion of rocks with coralline algae present was compared with respect to rock surface area and depth. The cumulative number of bryozoan species was recorded for rocks of each size class, from each depth, in order to try to estimate the effectiveness of sampling. If the cumulative species curve reached a plateau it was assumed that most of the species present in the local population had been sampled. Sampling effectiveness was also investigated by recording the cumulative number of colonies counted. This was because only few large rocks were present in samples, but these might sometimes be encrusted with hundreds of colonies.

Observations were made on the intra- and inter-specific interactions between all bryozoan species for each rock. Overgrowth was recorded as occurring when the elevation of the growing edge covered the apertures of the competitor, a tie was recorded when

overgrowth took place by both competitors (i.e., there was no systematic outcome along the contact zone), or growth ceased along the contact zone (Stebbing 1973). Overgrowth interactions were only recorded for meetings between growing edges (with limits between 330° - 30° contact angle) termed 'frontal', and were not recorded if the overgrown colony was dead beforehand, if one colony had been completely overgrown or if overgrowth occurred because one colony had settled directly onto another (see Rubin 1982, Turner & Todd 1994).

A win/loss ratio was calculated for each bryozoan species where more than 5 interactions were identified (as in Jackson 1979a), and these were tabulated with details of zoarial type (zooid growth morphology), ability for erect growth, number of spines in marginal zooids, fouling resistance and colony thickness. These data were taken so as to relate competitive ability to the morphological characteristics of each species (Lopez Gappa 1989).

Statistical analysis

The proportions of decided outcomes of intra-specific interactions were analysed in relation to species, depth, win/loss ratio and proportion of colonies on the upper rock surface using logistic regression (Cox 1970, Hosmer & Lemeshow 1989, Trexler & Travis 1993). Overdispersion (or extra-binomial variation) in the proportions was detected across species, and so the method of Williams (1982) was used to adjust standard errors in testing for trends. Inter-specific interactions were analysed separately for each species in relation to competitor, depth and surface area in two ways. Firstly, the relative frequencies of the three possible outcomes (win, tie, loss) were analysed using log-linear models to test for effects of competitor, depth and surface area (McCullagh & Nelder 1989, Turner & Todd 1994). Secondly, because most interactions were decided (there were only about 4% ties), the proportion of wins was analysed using logistic regression to test for competitor effects and for trends with depth and surface area. In a further analysis of the pairwise interactions, the probability of a given outcome between a pair of species was described by a Bradley-Terry model (McCullagh & Nelder 1989) in which:

$$Pr(\text{species } i \text{ defeats species } j) = \frac{\exp(s_i - s_j)}{1 + \exp(s_i - s_j)}$$

A competitive ranking of the species was obtained from the estimated values of the species effects (s_i) in the fitted model. This procedure allows for a different set of competitors for each species and a variable number of interactions between pairs of species, both of which could produce bias in a crude sample ranking. Analyses were performed using the statistical package Genstat 5 (Genstat 5 Committee 1987).

Results

Representatives of seven encrusting animal phyla, including a total of 21 species of encrusting cheilostomatid bryozoans, were present on the rocks analysed. Red algae were also abundant. Polychaetes (mostly spirorbids) dominated the encrusting fauna of the substrata at the shallowest three locations surveyed, whereas bryozoans dominated at the three deepest (Table 4.1). Cnidarians, entoprocts and brachiopods were also present in addition to those groups listed in Table 4.1, although all were very minor occupiers of space.

Table 4.1

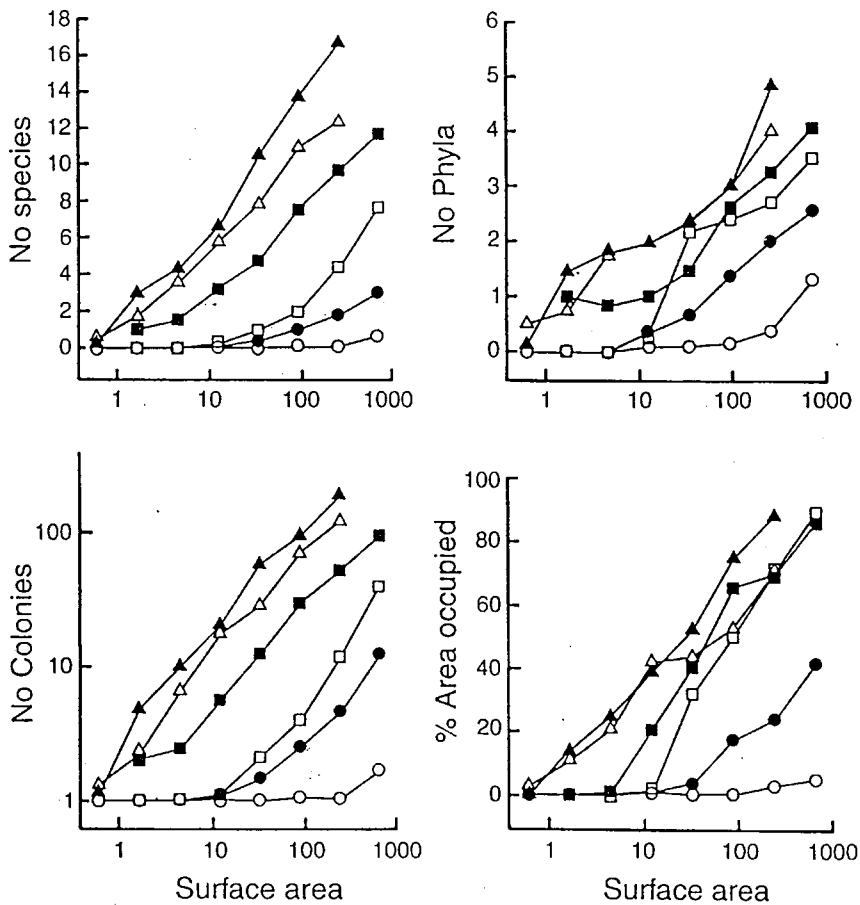
The dominant faunal taxa at each depth, for rocks of all sizes pooled by depth. Data are the percentage of all rocks on which the three taxon groupings were the dominant space occupiers. No other taxa dominated the rock surface area on rocks of any surface area at any depth.

Depth (m)	% rocks for which taxon is dominant fauna		
	Polychaetes	Bryozoans	Sponges/Tunicates
0	98	2	0
6	86	14	0
12	82	17	1
24	7	92	1
34	5	94	1
42	9	89	2

Taxonomic richness, measured both in terms of number of phyla and number of bryozoan species, increased with both rock surface area and depth (Figure 4.2a,b). The number of bryozoan colonies and the total area occupied also increased with substratum surface area and depth (Figure 4.2c,d). Whilst there was little difference in % cover of substrata between the sites at 12 m and deeper, peak coverage of the largest rocks at 6 m was, at approximately 40%, less than half that of the deeper substrata, and peak occupation of the intertidal rocks was below 5%. The largest rocks from the intertidal were broadly similar in all of the measured degrees of colonisation to the smallest rocks from 42 m.

Figure 4.2

Number of bryozoan species, phyla and bryozoan colonies, and percent area occupied by colonists with rock surface area (log scale) and depth. The depths are: ○ = intertidal, ● = 6 m, □ = 12 m, ■ = 25 m, △ = 34 m, ▲ = 42 m.



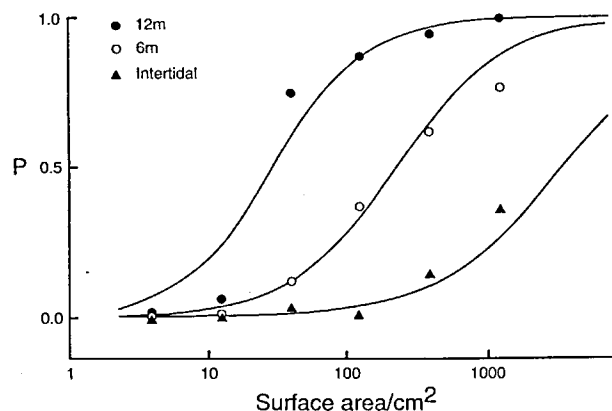
The shallow sublittoral at Signy Island is frequently disturbed by wave action, currents, and probably of greatest influence, ice (Peck & Bullough 1993, Barnes 1995a, b). Whilst the actual frequency of rock turnover could not be quantified, coralline algal growth on the upper surface of rocks was used as a surrogate measure. The probability of coralline algae (*Lithothamnion* sp.) presence on substrata was plotted for various size classes of rocks for the depths 0 (intertidal), 6 and 12 m. The points and fitted logistic models (Figure 4.3) imply that coralline algal presence is a useful surrogate measure of the relative change in turn over or disturbance rate with surface area and depth. Rocks from the deeper sites were not analysed because of complexities of light attenuation and sedimentation, as well as the suggestion (Figure 4.2d) that the influence of disturbance was strongest between 0 and 12 m.

Figure 4.3

Probability of the coralline alga *Lithothamnion* occurring on a rock with rock surface area (log scale) and depth. The depths are ▲ = intertidal, ○ = 6 m, ● = 12 m. The fitted lines follow the logistic equation

$$P = e^L / (1 + e^L)$$

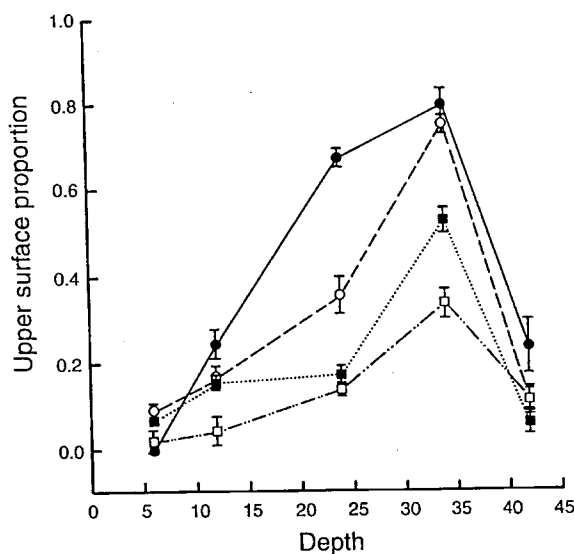
where $L = -8.32 + 1.12 (\ln A) + 0.28 (D) + 0.33 ((\ln A) \times D)$, A = surface area of rock (cm^2) and D = Depth (m).



Most of the colonisation by faunal elements was on the undersurface of rocks, whilst coralline algae, as discussed above, dominated the upper surface. Approximately 80% of the total number of bryozoan colonies on rocks at each depth (except at 34 m which was $\approx 55\%$), colonised the under-surfaces.

Figure 4.4

Proportion of population on the upper rock surface or overgrowing coralline algae with depth, for four species of encrusting bryozoans. The species are ● = *Ellisina antarctica*, ○ = *Celleporella bougainvillei*, ■ = *Inversiula nutrix*, □ = *Escharoides tridens*. Bars represent standard errors.



The majority of bryozoan species in this study showed an increase in number of colonies occurring on the upper surface of rocks with depth down to 34 m, and then a decrease at 42 m, although the magnitude of increase varied between species (Figure 4.4). The decrease in the proportion of upper surface colonies at 42 m was probably associated with the higher level of sedimentation occurring on rocks at this depth (pers. obs.).

Sampling effectiveness

Cumulative counts of the number of bryozoan species plotted against sample (rock) number illustrated that the true number of species present in the population had probably been recorded from the small and middle sized rocks, but not for the larger size class (Figure 4.5a). When plotted out in terms of numbers of colonies sampled, all size classes seemed similarly effective (Figure 4.5b). It is probable that most species were represented.

Figure 4.5a

Cumulative number of bryozoan species with rock sample number, for rock size classes: \square = $<50\text{ cm}^2$, \bullet = $50\text{--}100\text{ cm}^2$ and Δ = $>100\text{ cm}^2$, at depths of 0 m, 6 m, 12 m, 25 m, 34 m, 42 m.

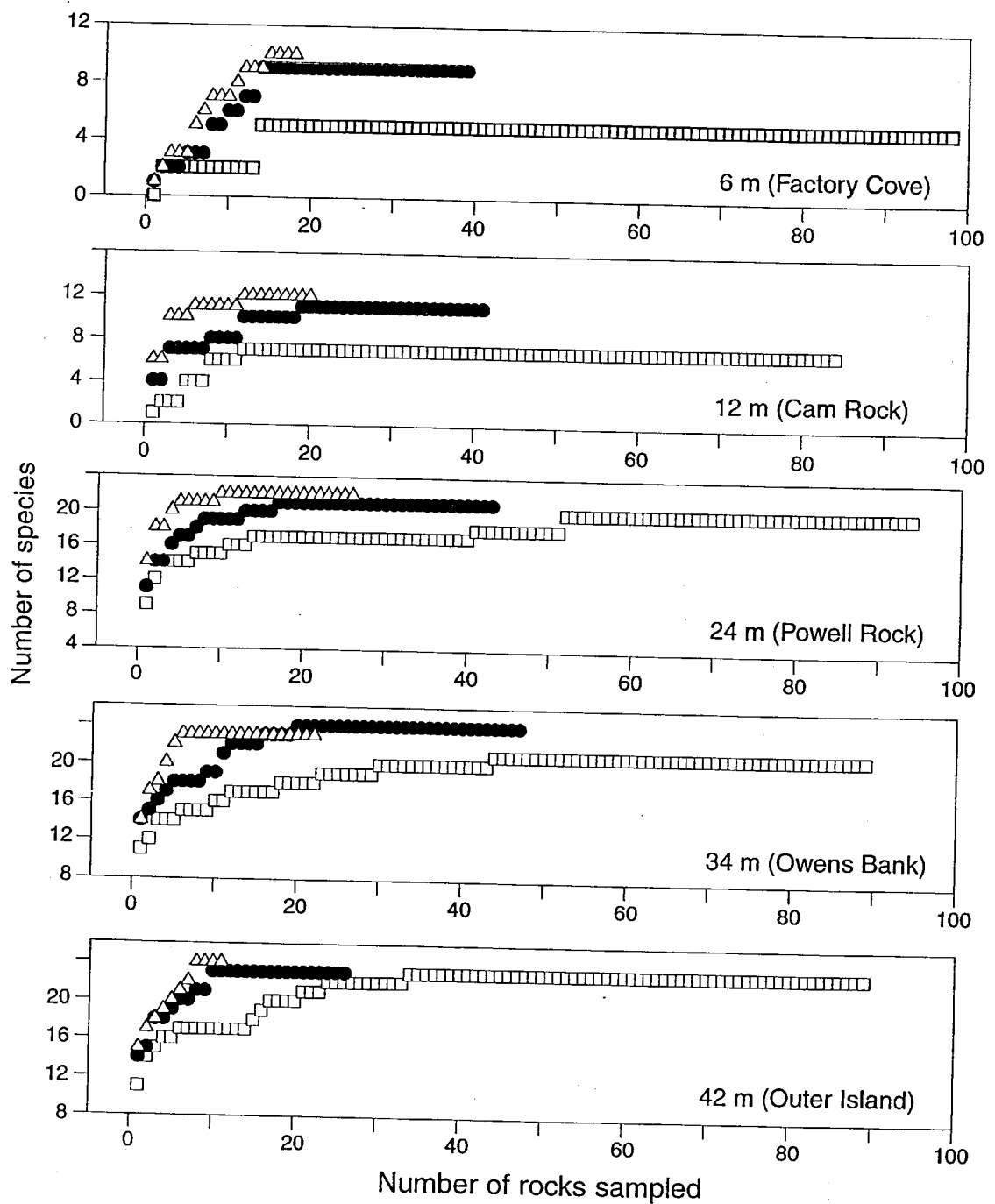
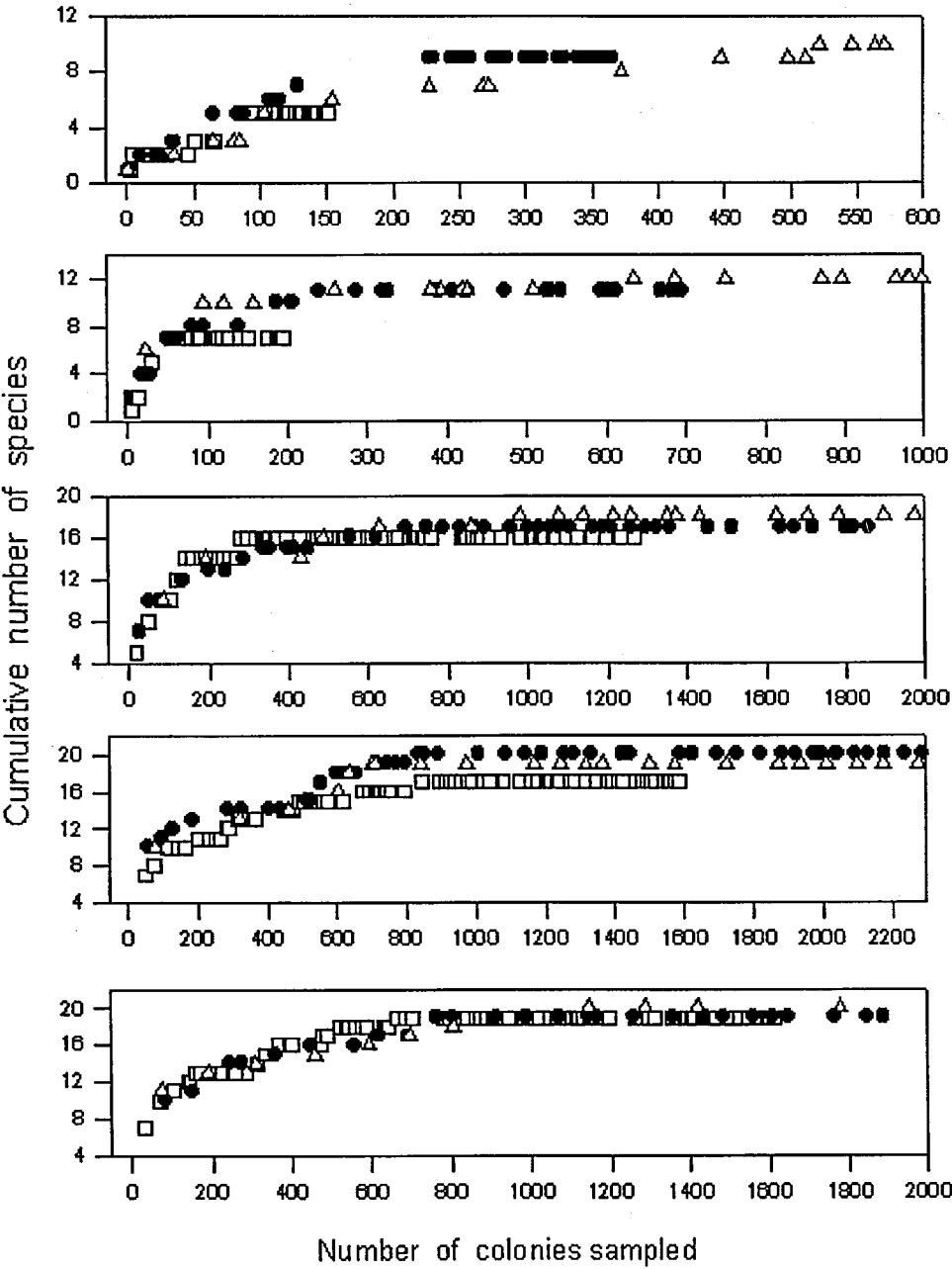


Figure 4.5b

Cumulative number of bryozoan species recorded with bryozoan colony sample number, for size classes: \square = $<50\text{ cm}^2$, \bullet = $50\text{-}100\text{ cm}^2$ and Δ = $>100\text{ cm}^2$, at depths of 0 m, 6 m, 12 m, 25 m, 34 m, 42 m.



Between species interactions

A total of 4076 competitive interactions were recorded between the 21 species of cheilostomatid bryozoans. The data from all the depths pooled are illustrated in the form of a species matrix in Table 4.2. One species, *Harpecia spinosissima* (Calvet), is absent from the matrix as no competitive interactions were observed involving this species.

Interspecific competition accounted for the majority (83.6%) of the 4076 interactions observed, 98% of which resulted in decided outcomes (Table 4.2). Although the outcome of any individual interaction was almost always a win for one of two competing colonies, a less distinct pattern emerged when these interactions were examined on a species by species basis. Over half (76) of the 145 species-pair interactions observed (190 species-pair interactions were possible) had indeterminate overall results (neither species won all encounters). Thus if two species encountered each other on a number of occasions, even though each encounter produced a decided outcome, the pattern by species was not always determinate (one species wins some encounters, the second species others). The number of determinate species-pair interactions in this study was probably overestimated, since 43 of the 64 species-pair interactions with determinate results involved fewer than five observed interactions. The influence of site depth, rock surface area and specific competitor on the outcome of interspecific competition was examined for each species. Encounter angle, which has been shown to influence the outcome of some species-pair interactions (Rubin 1982, Turner & Todd 1994), was not included as a variable in this study, as only frontal interactions were considered. Since virtually all colonies were circular, frontal interactions appeared to constitute the majority of all meetings, as was also found by Lopez Gappa (1989).

The analysis using log-linear models showed that the dominant effect on the outcome of interspecific interactions for all species tested was the identity of the competitor, and that depth and rock surface area accounted for relatively little variation (Table 4.3). However, the logistic regression of the proportion of wins (Table 4.4) detected a statistically significant increase with depth for *Ellisina antarctica* Hastings (Deviance X_1^2

Table 4.2

Matrix of competitive interactions between the 20 species of bryozoans involved in more than 5 interactions in total. For each cell the top left, top right and bottom left data give, respectively, the number of ties between species A and B, wins by B (=losses by A) and wins by A (=losses by B). The number in the bottom right of each cell is the total number of interactions for that pair.

	B. erecta	K. antarctica	V. laia	A. inchoata	S. mitina sp.	A. familiaris	L. lyulata	M. brevissima	E. antarctica	L. nutrix	L. eatoni	E. tridens	S. rogiackae	M. stenopora	H. inerma	C. dictyota	C. bougainvillei	A. antarctica	F. rugula	C. antarctica
Beania erecta waters	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Klugerella antarctica (Kluger)	2	5	1	1	35	35	4	2	27	27	12	20	3	3	9	17	7	1	1	22
Valdemunitella laia (Kluger)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arachnopusia inchoata Hayward & Thorpe	1	2	0	1	1	10	4	1	15	7	3	3	3	3	3	3	3	3	3	3
Smittina sp.	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiblestrum familiaris Hayward	9	6	1	1	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lageneschara lyulata (Calvet)	8	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micropora brevissima waters	14	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ellisina antarctica Hastings	33	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inversula nutrix Jullien	36	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacema eatoni (Buck)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Escharoides tridens (Calvet)	50	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smittina rogiackae Hayward & Taylor	12	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microporella stenopora Hayward & Taylor	6	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippodanella inerma (Calvet)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Celleporella dictyota Hayward	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Celleporella bougainvillei (d'Orbigny)	32	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Almulusia antarctica (Powell)	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fenestrulina rugula Hayward & Ryland	6	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Celleporella antarctica Moyano & Gordon	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

= 13.2, $p < 0.01$). Since a depth effect was found for only one of the 20 species examined, interaction data was pooled for all depths and rock surface areas (Table 4.2) to examine species competitor relationships in more detail.

The overall incidence of ties in interspecific meetings (2%) was very low compared with those of intraspecific meetings (63%) and, as might be intuitively expected, was related to how close species were in terms of competitive ability (Figure 4.6). The relatively low proportion of ties, reversals in outcomes, or 'loops' (8%, over half of which include species pairings with fewer than 5 observed interactions) and the high incidence of determinate species-pair interactions suggests a predominantly transitive pattern or competitive hierarchy (Petraitis 1979, Buss & Jackson 1979). Intransitive patterns generally lead to no single ultimately dominant species, although species may be separated into broad groups of similar competitive ability. Although there was some degree of intransitivity in a number of species, the assemblage could be clearly ranked in sequence, from a species nearly always overgrown by others (*Celleporella antarctica* Moyano & Gordon) to one almost completely dominant (*Beania erecta* Waters).

The index of intransitivity proposed by Rubin (1982) gave a value of 4.61, which is close to the theoretical maximum value for perfect transitivity with 10 species (5.97) (only 10 species could be used because one of the conditions of use of this index is that all species must encounter each other at least once). Whilst the competitive rankings in this assemblage lay in the continuum between transitive and intransitive, they are clearly predominantly hierarchical.

The crude sample rankings in Table 4.2 may deviate from true population rankings, as the set of competitors was not the same for each species and the number of interactions varied between pairs. Thus the ranking of each species may be weighted towards the competitors with which they have had the most frequent encounters. An extrapolated set of rankings was obtained using the Bradley-Terry model (see statistical analysis section), which assumes transitive properties in the assemblage modelled (Table 4.5). The model showed a close fit to the actual data, as no species differed by more

than one rank between the observed data and fitted model.

Table 4.3

Summary of the analysis of interspecific interactions with outcomes (win, tie, lose) using log-linear models to test for effects of competitors, depth and rock surface area. Table shows reduction in deviance due to including different terms in the model (degrees of freedom shown in brackets). Statistical significance: * - $P < 0.05$; ** - $P < 0.01$; *** - $P < 0.001$.

Species	Reduction in deviance due to fitting different effects				
	Outcome x Competitor	Outcome x Depth		Outcome x Surface Area	
		Before competitor	After competitor	Before competitor	After competitor
<i>Arachnopusia inchoata</i>	*** 212.4 (24)	6.9 (8)	11.3 (8)	* 11.4 (4)	1.4 (4)
<i>Amphiblestrum familiaris</i>	*** 43.2 (16)	* 12.8 (6)	3.7 (6)	7.3 (4)	4.8 (4)
<i>Micropora brevissima</i>	*** 181.3 (22)	8.6 (6)	6.3 (6)	4.4 (4)	2.7 (4)
<i>Ellisina antarctica</i>	*** 132.7 (20)	* 15.8 (6)	** 17.7 (6)	8.0 (4)	4.1 (4)
<i>Inversiula nutrix</i>	*** 226.0 (22)	** 23.8 (8)	13.8 (8)	2.8 (4)	1.8 (4)
<i>Lacerna eatoni</i>	* 24.9 (14)	1.1 (4)	1.2 (4)	4.7 (4)	5.0 (4)
<i>Escharoides tridens</i>	*** 313.8 (26)	** 28.2 (8)	6.1 (8)	* 11.0 (4)	4.9 (4)
<i>Smittina rogickae</i>	*** 55.1 (16)	4.6 (4)	2.0 (4)	3.9 (4)	5.0 (4)
<i>Celleporella bougainvillei</i>	*** 49.6 (14)	6.8 (8)	3.5 (8)	** 18.4 (4)	** 15.2 (4)
<i>Fenestulina rugula</i>	*** 87.4 (22)	3.2 (2)	0.9 (2)	** 16.6 (4)	5.0 (4)

Table 4.4

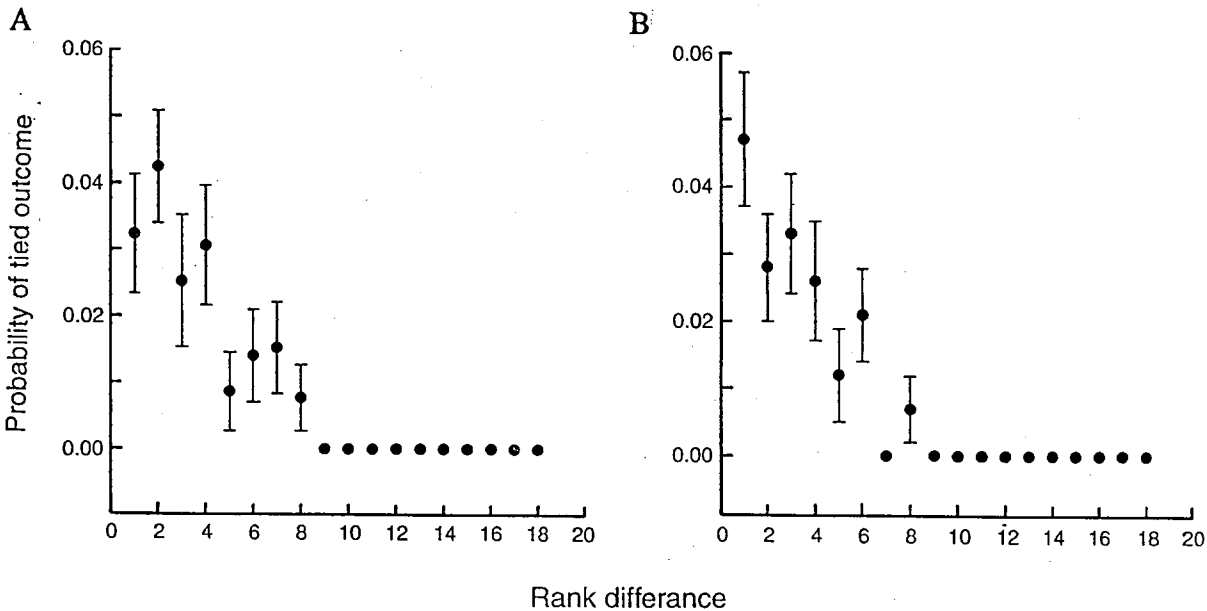
Summary of the analysis of proportion of wins in interspecific interactions using logistic regression to test for effect of competitors, and trends with depth and rock surface area (degrees of freedom shown in brackets). Statistical significance: * - $P < 0.05$; ** - $P < 0.01$; *** - $P < 0.001$.

Species	Reduction in deviance due to fitting different effects				
	Competitor	Depth		Surface Area	
		Before competitor	After competitor	Before competitor	After competitor
<i>Arachnopusia inchoata</i>	*** 95.8 (10)	* 10.0 (4)	6.4	2.3 (2)	0.4
<i>Amphiblestrum familiaris</i>	*** 31.0 (8)	** 11.9 (3)	2.8	0.9 (2)	2.3
<i>Micropora brevissima</i>	*** 153.7 (10)	* 11.0 (3)	6.0	3.1 (2)	2.2
<i>Ellsina antarctica</i>	*** 115.3 (8)	** 13.9 (3)	** 14.3	4.8 (2)	3.8
<i>Inversiula nutrix</i>	*** 204.4 (10)	*** 21.2 (4)	* 11.9	0.6 (2)	0.3
<i>Lacerna eatoni</i>	* 18.2 (6)	0.6 (2)	0.9	0.7 (2)	1.9
<i>Escharoides tridens</i>	*** 266.0 (11)	*** 23.2 (4)	3.9	5.2 (2)	2.0
<i>Smitlina rogickae</i>	*** 45.4 (7)	2.1 (2)	0.6	2.9 (2)	2.0
<i>Celleporella bougainvillei</i>	*** 41.6 (7)	5.3 (4)	1.6	5.6 (2)	4.4
<i>Fenestrulina rugula</i>	*** 69.1 (8)	3.4 (1)	0.4	1.0 (2)	3.1

As observed in studies of bryozoan competition at lower latitudes (Jackson 1979b, McKinney & Jackson 1991) a wide range of morphological strategies were employed by different species at the points of contact between colonies. Often this involved extra spines (*Aimulosia antarctica*), raising the growing margin from the substratum (*Amphiblestrum familiaris*), growing a basal sheet of skeletal tissue ahead of the normal zooids (*Escharoides tridens*) or growing erect temporarily to grow over the front margin of the competitor without contact until several rows of zooids back (*Arachnopusia inchoata*). The

Figure 4.6

Probability of a tied outcome in interspecific competition, as a function of rank difference between competitors (numerical difference in competitive rank as assessed from competitive interactions). a) actual data, b) data predicted from Bradley-Terry model. Bars are standard deviations.



ability to raise the colony margin and to grow at least temporarily erect was present in many of the better competitors, as was the ability to avoid fouling from other organisms (Table 4.6). The production of spines, however, appeared to confer no significant advantage (Spearman rank test, $r_s=0.01$, $P > 0.10$). Of the morphological characteristics measured, colony thickness or height from substratum was the main determinant of competitive ability ($r_s=0.61$, $P < 0.05$). Other factors such as the presence and size of avicularia may also be important in overall competitive ability, this was particularly so in the case of *Beania erecta* (which has two large avicularia per zooid). Of the top five competitors though, only one (*A. inchoata*) was abundant in this study. Over the range of substratum (rock) surface areas measured, competitive ability and area occupied were not significantly correlated ($r_s=0.06$, $P > 0.05$).

Table 4.5

Ranking of competitive ability in selected species based on actual scores observed and estimated win :lose scores using the Bradley-Terry model. *Beania erecta* and *Celleporella antarctica* were not included because of almost entirely determinate scores, and *Smittina* sp., *Lageneschara lyrulata* and *Celleporella dictyota* were not included because of involvement in few species pair interactions.

Species	initial rank	estimated rank
<i>Klugarella antarctica</i>	1	2
<i>Valdemunitella lata</i>	2	1
<i>Arachnopusia inchoata</i>	3	3
<i>Amphiblestrum familiaris</i>	4	4
<i>Micropora brevissima</i>	5	5
<i>Ellisina antarctica</i>	6	6
<i>Inversiula nutrix</i>	7	8
<i>Lacerna eatoni</i>	8	7
<i>Escharoides tridens</i>	9	9
<i>Smittina rogickae</i>	10	11
<i>Microporella stenopora</i>	11	10
<i>Hippadanella inerma</i>	12	12
<i>Celleporella bougainvillei</i>	13	13
<i>Aimulosia antarctica</i>	14	15
<i>Fenestrulina rugula</i>	15	14

Within species interactions

Intraspecific competition was observed in 16 species and accounted for 668 of the 4076 interactions observed, 63% of which resulted in tied outcomes. Tied outcomes or a simple cessation of growth were the most frequent outcomes of intraspecific meetings for most species, as has been found previously (Knight-Jones & Moyse 1961, Stebbing 1973, Osman 1977, Seed & O'Connor 1981, Cancino 1986, Lopez Gappa 1989, Turner & Todd 1994). In three of the 21 species, however, cessation of growth occurred only rarely. Intraspecific overgrowth occurred in two species (*Ellisina antarctica* and *Celleporella bougainvillei*), but *Arachnopusia inchoata* Hayward & Thorpe may obtain a bilaminar foliaceous colony form by colony margins growing against each other, and thus overgrowth does not occur.

Table 4.6

Relative abundance (Number of colonies and % area), win:loss ratio, growth form, ability to grow erect in addition to encrusting, number of spines in marginal zooids, resistance to fouling and colony thickness of the twenty bryozoan species involved in competitive interactions. Species arranged in order of decreasing win : loss ratio. N, % of total bryozoan colonies at 34 m; % Area, percentage of total area occupied by bryozoans; Growth form, SL = single-layered (* *Beania erecta* is single layered but with vertically orientated zooids), ML = multilayered, MS = Multiseries; Erect ability and fouling resistance both scored subjectively as ++ good, + some, - none. ND = No Data.

Species	N	% Area	W/L ratio	Growth form	Erect ability	Margin spines	Fouling resist	Colony thickness mm
<i>B. erecta</i>	0.2	0.2	140	SL*MS	+	2	++	1.20
<i>K. antarctica</i>	0.3	0.2	7.1	SL MS	+	2	+	0.38
<i>V. lata</i>	0.7	0.9	4.3	ML MS	++	0	++	ND
<i>A. inchoata</i>	7.5	8.7	4.2	ML MS	++	6+	++	0.38
<i>Smittina</i> sp.	<0.01	<0.01	2.4	SL MS	-	0	++	ND
<i>A. familiaris</i>	4.7	5.1	2.2	SL MS	-	2	+	0.19
<i>L. lyrulata</i>	<0.01	<0.01	1.9	ML MS	++	0	+	0.60
<i>M. brevissima</i>	9.3	10.0	1.8	SL MS	-	2	-	0.20
<i>E. antarctica</i>	6.4	7.0	1.5	SL MS	-	0	+	0.22
<i>I. nutrix</i>	15.1	16.2	0.9	SL MS	-	0	-	0.40
<i>L. eatoni</i>	0.9	1.3	0.8	SL MS	-	4	-	0.24
<i>E. tridens</i>	12.7	12.9	0.7	SL MS	-	3	-	0.33
<i>S. rogickae</i>	15.5	12.5	0.5	SL MS	-	0	+	ND
<i>M. stenoporta</i>	3.9	4.3	0.5	SL MS	-	2-3	+	ND
<i>H. inerma</i>	1.3	1.4	0.4	SL MS	-	0	-	0.24
<i>C. dictyota</i>	<0.01	<0.01	0.4	SL MS	-	0	-	0.20
<i>C. bougainvillei</i>	13.5	12.6	0.2	SL MS	-	2Small	-	0.24
<i>A. antarctica</i>	3.7	2.7	0.1	SL MS	-	4-7	-	0.17
<i>F. rugula</i>	4.0	4.1	0.1	SL MS	-	0	-	0.21
<i>C. antarctica</i>	0.3	0.1	-	SL MS	-	0	-	0.18

In five observed intraspecific meetings, three involving the species, *Fenestrulina rugula* Hayward & Ryland, and two involving the species *Microporella stenopora* Hayward & Taylor, a tied outcome had resulted not in cessation of growth, but in zooidal fusion (Homosyndrome) and reorientation of the growing margin. The result of such meetings was the production of a common growing edge from the two colonies.

Logistic regression of the proportion of decided outcomes showed a large and statistically highly significant effect of species, and trends with depth, ratio of colonies on upper rock surface and win/loss ratio (Table 4.7). However, the ratio of colonies on upper rock surfaces varied with depth (Figure 4.4) and their effects could not be separated in models containing both variables. The effect of win/loss ratio was negligible within species.

An analysis of trends of the ratio of colonies on upper rock surface and win/loss ratios at each depth failed to detect any statistically significant effects. However, a large percentage of the variation was due to the inclusion of one species: *Arachnopusia inchoata*. The morphology of *Arachnopusia inchoata* (as well as the rare *Valdemunitella lata* and *Lageneschara lyrulata*) was such that the concept of decided or tied outcomes as applied to the other encrusting species was not applicable, since bilaminar growth could result instead (see discussion in methods). When this species was excluded from the analysis, the proportion of decided outcomes increased with the ratio of colonies on upper rock surface: depth 34, $t_6 = 2.68$, $P < 0.05$; depth 42 $t_3 = 3.24$, $p < 0.05$ (allowing for extra-binomial variation, see statistical methods).

Summary of results

Polychaetes and bryozoans dominated the fauna colonising the rocks studied, although representatives of five other phyla were present. The number of phyla and percentage area of space occupied increased with both rock surface area and depth. The number of bryozoan species and colonies on substrata increased similarly. Most of the fauna occurred

on the lower surfaces of substrata, whereas coralline algae often dominated the upper surface. The proportion of bryozoans colonising the upper surface of substrata increased with depth (but declined at 42 m, probably due to local sedimentation). The samples of all size classes at all depths probably contained most of the bryozoan species occurring within these localities.

Table 4.7

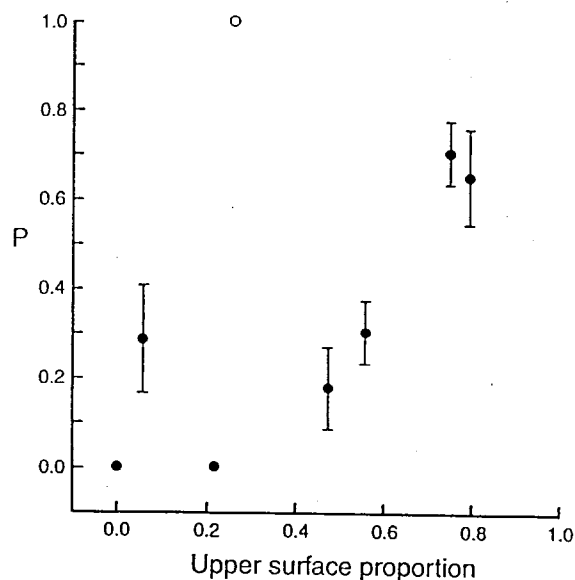
Summary of logistic regression analysis of the proportion of decided outcomes in intraspecific interactions. Table shows reduction in deviance due to including different terms in the model with effects for species (16 degrees of freedom), linear and quadratic trends in depth, and linear trends in proportion of colonies on upper rock surface and win:loss ratio. Species effects were marked and are included in all models with two or more variables. Statistical significance: * - $P < 0.05$; ** - $P < 0.01$; *** - $P < 0.001$

No. terms in model	Species	Terms in model			
		Depth		Prop. upper rock Surface	Win/loss ratio
		Linear	Quadratic		
1	174.5 ***	-	-	-	-
1	-	0.93	10.60 **	-	-
1	-	-	-	23.23 ***	-
1	-	-	-	-	65.50 ***
2	181.1 ***	1.71	4.90 *	-	-
2	157.1 ***	-	-	5.77 *	-
2	108.9 ***	-	-	-	0.00
3	157.5 ***	0.95	0.77	0.11	-
3	101.01 ***	1.71	5.22 *	-	0.32
3	76.96 ***	-	-	5.77 *	0.00
4	76.90 ***	1.18	0.57	0.590	0.80

Over 4000 bryozoan-bryozoan interactions were analysed. Intraspecific or within species interactions made up fewer than one sixth of these, and most resulted in tied outcomes. Significant differences in the outcome of intraspecific competitive interactions occurred across species (Deviance $\chi^2_{16} = 76.87$, $P < 0.001$) after allowing for possible relationships with win to loss ratio, depth and rock surface. Analyses of intraspecific competition across species suggested that species with a higher proportion of colonies on the upper surfaces of rocks showed a higher probability of a decided outcome (Figure 4.7).

Figure 4.7

Probability of a decided outcome (in interspecific competition) with proportion of population occurring on upper rock surfaces, for eight species of encrusting bryozoans at 34m. Bars are standard errors based on binomial sampling. Open circle represents the species *Arachnopusia inchoata*, which has important morphological differences from the other species (see text).



The outcome of interspecific interactions varied principally with competitor effects, but little with depth and substratum surface area. The probability of tied outcomes was related to how closely ranked competitors were in terms of competitive ability. As reversed outcomes as well as ties were rare, a predominantly transitive pattern or competitive hierarchy was indicated. The constituent species were ranked according to win/loss ratio, and demonstrated a very broad range of competitive ability. Various morphological changes were observed in marginal zooids at contact points between colonies, which may have influenced the outcomes, but of the variables measured, colony thickness (height above the substratum) was the main determinant of outcome. The observed areas occupied by bryozoans was not correlated with competitive ability.

Discussion

Although extensive benthic communities, often largely sessile, have been documented at various sublittoral locations within Antarctica (White & Robins 1972, Oliver *et al.* 1976, Voß 1988, Kirkwood & Burton 1988, Rauschert 1991, Galéron *et al.* 1992), for logistic reasons few studies of such communities have yet been undertaken. Bryozoans were described in chapters 2 and 3 as major occupiers of space on sublittoral rock faces at Signy Island, particularly in areas of frequent disturbance. Thus a key area for research, in bryozoan communities in particular, is on smaller scale unstable substrata. To date however, small scale studies of benthic Antarctic communities have relied on artificial substrata (Dayton & Oliver 1978, Rauschert 1991), and little is known of benthic community ecology on natural small substrata.

Narrow temperature and salinity fluctuations characterise the Antarctic marine subtidal environment, whereas those few species which inhabit the intertidal location must survive nearly five times the total sublittoral annual variation in temperature within a few hours (pers. obs.). These organisms such as bryozoans and hydroids inhabiting the intertidal must also survive very low salinities from glacial run off during the summer and raised salinities immediately below sea-ice in winter (Cox & Weeks 1974). Although most Antarctic marine invertebrates appear to be stenothermal and stenohaline (Rakusa-Suszczewski & McWhinnie 1976, Peck 1989), a few predominantly sublittoral species have sufficiently wide physical tolerances to allow colonisation and survival of the extremes in the Antarctic intertidal zone (Davenport 1988).

On rocks of larger surface areas, especially at the deeper locations, up to six animal phyla were present, but the total area occupied by most was small and the spectrum of substrata examined generally illustrated the early developmental stages in epifaunal colonisation. Analysis of the incidence of coralline algal growth on substrata with respect to surface area and depth, suggests that the presence of coralline algae is a valid proxy of turnover or disturbance rate. Polychaetes dominate the most frequently disturbed rocks (i.e.

those at shallow depth or of small size), whereas bryozoans dominated the larger and deeper rocks. Although bryozoans overgrew the tubes of polychaete colonisers, the switch in area/ dominance had little to do with this. Polychaetes occupied similar, but small, areas on rocks of similar size at most depths, whereas bryozoans occupied proportionally very little area on the more disturbed rocks, but almost covered those which were less disturbed. Much of the bryozoan growth was expansion over unoccupied rock surface. Other animal groups such as sponges and ascidians colonised only the largest and deepest rocks (i.e. the more stable substrata) and as a result usually had to overgrow other colonisers.

Sponges and ascidians, whose observed small scale distribution suggest limited powers of dispersal, but which are better overgrowth competitors, have been found to occupy a proportionally larger fraction of less disturbed substrata, such as rock faces adjacent to the loose rocks (chapter 3) as would be expected from the results of this study. Rock faces in these localities can be regarded as end points in substratum stability series, although they are still subject to wave and ice disturbance, and are thus likely to be the sites of greatest local hard substratum community development. The broad community sequence observed with increasing stability in this study; algae-polychaetes-bryozoans-sponges/ ascidians, was found to occur with increasing depth (and hence by implication the time since the most recent physical disturbance) on rock faces (chapters 2 & 3). This sequence also illustrates the change from the dominance of solitary organisms on newly available substrata to that of colonial forms on more stable substrata, as has been well documented at lower latitudes (Jackson 1977, Buss 1979, Buss & Jackson 1979, Woodin & Jackson 1979). Artificial substrata studies suggest that at this latitude the time span of community development to achieve 100% cover of the substrata, and to have the taxonomic diversity found on the larger rocks, may be in the region of decades (chapter 5).

The data from this study are inconclusive as to whether the interspecific win/loss ratio is related to the outcome of intraspecific competition. This was partly due to the rarity of good competitors and the confounding factor of distribution between upper and lower surfaces. The results from species which may achieve a bilaminar growth form, such as *Arachnopusia inchoata* and *Lageneschara lyrulata*, may be best treated separately as

such a growth form is a forth possible outcome of two colonies meeting, but one which is not possible between purely encrusting forms.

The incidence of zooidal fusion was too infrequent to provide evidence of increased relatedness of same-species neighbours on rock undersurfaces, although the five examples all occurred on the lower surface of rocks. Homosyndrome (Knight-Jones & Moyse 1961) has been previously observed in *Fenestrulina* sp. at lower latitudes (Craig 1994), as well as in a number of other species e.g., *Membranipora hyadesi* (Moyano 1967), *Parasmittina nitida* (Humphries 1979) and *Umbonula alvareiziana* (Lopez Gappa 1989).

The interspecific interactions within the 20 species of cheilostomes found, whilst showing a small degree of intransitivity, essentially formed a clear hierarchy with a single competitive dominant, (cf Gilpin 1975, Jackson & Buss 1975, Jackson 1979a). The interactions, when subjected to the most recently suggested transivity indices (Tanaka & Nandakumar 1994), yield a win index of 0.85 and a stand-off index of <0.01 . Such values indicate a more transitive system than those found by Lopez Gappa (1989) or Tanaka & Nandakumar (1994), both of whom describe the ranking of their assemblages as "hierarchically dominant". Intransivity has been argued to be likely in multi-phyletic assemblages with more ways of interaction (Buss & Jackson 1979) and in particular within bryozoan assemblages where many aspects influence potential outcome (Quinn 1982). An increase in intransivity has also been shown moving from frontal through lateral to rear encounters (Rubin 1982, Turner & Todd 1994) and with change in size of competitors (Buss 1980, Russ 1982, Sebens 1986). Although competitor size was not considered in this study and scores were only used from frontal interactions (which did however form the majority of interactions), the presence of large areas completely dominated by the species *Beania erecta* on adjacent rock faces provides evidence of a single ultimately dominant species (chapters 2 & 3). Evidence from the present study, as well as that from local rock faces and artificial substrata, suggests that the encrusting phyla were also essentially hierarchical: thus bryozoans overgrew polychaetes, and sponges overgrew bryozoans, with few reversals (chapter 6), and confirms the similar results of Russ (1982) and Lopez Gappa (1989). The high frequency of physical disturbance at this location is thus important in

maintaining high phyletic and species diversity.

Relatively few studies of competitive interactions between species assemblages have considered the influences of site and disturbance, between either different intertidal sites or intertidal and shallow sublittoral (Sebens 1986, Turner & Todd 1994). The present study has provided a comparison of a series of depths, disturbance levels and, by inference, stop points in time for community development and dynamics. Although community development altered substantially along disturbance axes, the competitive ability and overall win/loss ratios of individual species changed little, despite encountering a variety of different species with depth. Yearly and seasonal variation has been suggested as a possible source of variation in growth rates of species and therefore overgrowth potential (Seed & O'Connor 1981, Sebens 1986, Turner & Todd 1994). The annual feeding duration of certain bryozoan species at Signy Island certainly differs, as does growth, and thus may provide a competitive advantage to species such as *Arachnopusia inchoata* compared with other species (eg *Inversiula nutrix*) which feed and grow for shorter periods (chapter 8).

The relative abundance of species in this study was not correlated with competitive ability because most good competitors were rare, as found in other studies of communities in early developmental stages (Jackson 1979a, Lopez Gappa 1989). Studies of bryozoan assemblages in the later stages of development, however, found that strong overgrowth competitors dominated the space occupied (Keen & Neill 1980). The most abundant species, *Celleporella bougainvillei* and *Inversiula nutrix*, achieve success in different ways (Table 4.8). The three species of *Celleporella* all have low win/loss ratios (Table 4.6) but in the case of *Celleporella bougainvillei* colonises newly available or frequently disturbed substrata more quickly than other species, and also disperses colonies on a single rock quicker. Other species of *Celleporella* were also found in great abundance but with low overgrowth scores by Lopez Gappa (1989) and thus the strategy may apply through many species of the family. The colonisation values for *Inversiula nutrix* were quite high, and although this species had a middle range overgrowth score, because good competitors were rare, its colonies became large and occupied a high proportion of the total available area.

Table 4.8

The top three bryozoan species with the highest colonisation and growth scores, from pooled data, over all rock surface areas and depths. Species with greatest mean number of colonies per rock, far left top; species on greatest number of rocks, left top; species occupying most area per number of colonies per rock, right top; species with greatest win/loss ratio, far right top.

Colonisation		Growth	
Colony number/ rock	Number of rocks on which present	Area occupied/ no. of colonies	Overgrowth score
<i>C. bougainvillei</i>	<i>I. nutrix</i>	<i>I. nutrix</i>	<i>B. erecta</i>
<i>I. nutrix</i>	<i>C. bougainvillei</i>	<i>M. brevissima</i>	<i>K. antarctica</i>
<i>F. rugula</i>	<i>E. tridens</i>	<i>E. tridens</i>	<i>V. lata</i>

Zooid deterioration and fouling by spirorbid polychaetes and other bryozoans was common in *Inversiula nutrix*, although colonies frequently grew in fans back over themselves, covering older zooids, as described for *Steginoporella* (Jackson 1979a). *Arachnopusia inchoata* was by far the most abundant good competitor, probably as a result of faster colonisation and higher growth rates than the other strong competitors.

The concept of trade-offs between competitiveness and colonisation speed (as well as other attributes) and of disturbance-linked diversity has been discussed at great length by ecologists, particularly with respect to plant communities. Strategy and habitat modelling of botanical systems by Grime (1977), Southwood (1977), Tilman (1982), Greenslade (1983) and Sibly & Calow (1985) has developed considerably in dimensional complexity from the r-K formulation of MacArthur & Wilson (1967). The bryozoan examples discussed above illustrate that such concepts fit well with the species and community characteristics in the marine assemblage studied at Signy Island. Despite the high disturbance levels (Peck & Bullough 1993, Barnes 1995a,b) in the sublittoral maritime Antarctic, recent studies are providing evidence to challenge traditional ideas on ecological 'harshness' (Barnes & Clarke 1994, 1995a).

Competitive ability has been attributed to various morphological features (Jackson 1979a), although colony thickness (or vertical height above substratum) was one of the

most important (Buss 1980, Lopez Gappa 1989), as was found in this study. Vertical relief of certain species could be altered by behavioural adaptations (such as that described for *Inversiula nutrix* above) and species that predominantly settle on other colonisers (such as *Beania erecta* and *Klugarella antarctica*). The ability to elevate the colony margin away from the substratum, which was most common in species with bilaminar potential (e.g., *Valdemunitella lata*, *Arachnopusia inchoata* and *Lageneschara lyrulata* in this study), was an important aid to both overgrowth of other species and avoidance of overgrowth by other species. This feature enabled the bryozoan *Arachnopusia inchoata* occasionally to overgrow sponges (the only bryozoan observed to do this at Signy Island) as reported for other species with this ability (Jackson & Buss 1975, Jackson 1979b). Other structures unique to individual species (which are obviously difficult to compare between species) may also have a significant influence on the outcome of certain competitive interactions.

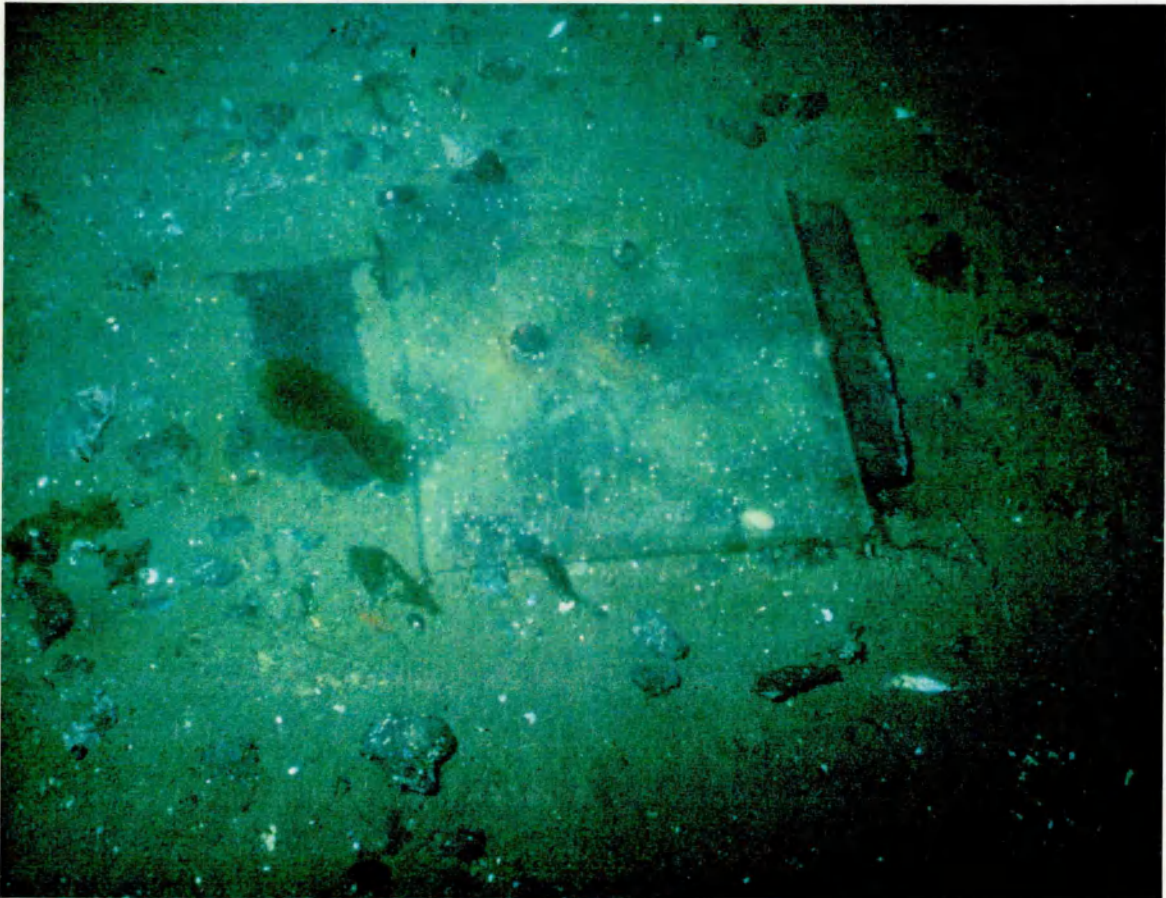
Whilst there was a significant increase in the relative numbers of bryozoan colonies occurring on the upper surfaces of rocks with depth, other animal groups remained on the lower surfaces. The increase in upper surface colonisation may reflect greater survival through decreasing wave and current disturbance, or decreasing overgrowth from coralline algae because of light attenuation with depth. Upper surface colonisers presumably gain advantages in greater space and therefore lower probability of interspecific competition as well as greater opportunities for larval dispersal. Of the two species most common on the upper surfaces, one was a good overgrowth competitor and the other poor. Since about 50% of the total available space was utilised on small rocks, escape from competition may be a major selective force influencing distribution. Increased larval dispersal may, however, be important to the results of intraspecific competition.

A statistically significant correlation across bryozoan species was noted between the probability of a decided outcome in intraspecific competition and the proportion of colonies of that species occurring on the upper surfaces of rocks (see Table 4.7). Thus, a meeting between two colonies of the same species was more likely to end in overgrowth if that species occurred predominantly on the upper surface. An interesting consequence of this relationship and larval dispersal opportunity is that of relatedness between neighbouring

colonies. Two colonies of *Ellisina antarctica* (a common upper surface species) are much less likely to be related, when considering larval dispersal in water currents over the surface of a rock compared to movement of a water-film under it, than two colonies of *Amphiblestrum familiaris* (an almost entirely lower surface species). The two most abundant upper surface species *E. antarctica* and *Celleporella bougainvillei* have also been noted as widely dispersed in the local sublittoral, occurring as two of the most abundant bryozoan species on other macroinvertebrates (chapter 6). Whilst there was some evidence for a similar trend within species (as opposed to across species as discussed above), separation of depth and surface influences was difficult and there were too few data points for each individual species. Obviously, if the explanation of larval dispersal, relatedness and intraspecific competition is true, then sufficient genetic data from different populations of the same species which exhibit different proportions of colonies on upper and lower surfaces, should illustrate this.

Plate 1

Settlement panel at 12 m showing colonisation by spirorbid polychaetes



Colonisation of artificial substrata: settlement panel studies

Introduction

Artificial substrata, usually perspex or slate panels, have been used widely to investigate many aspects of the ecology of community development on hard substrata. Such studies will simulate selected conditions found in natural substrata whilst providing more homogeneous conditions for analysis than natural conditions. Long term studies have been particularly valuable in determining the seasonal and annual variability of settlement and recruitment, and also the pattern of colonisation with time. Many of these studies have concentrated on interpreting the early development of fouling communities. The sequential series of colonisers observed, were initially described as proceeding in an orderly directional manner, termed 'succession' (Clements 1916, McCormick 1968, Odum 1969, Drury & Nisbit 1973, Horn 1974). More recently evidence from a number of studies has suggested that the pattern of community development is often more complex than a simple succession, involving seasonal larval abundance, timing of reproductive cycles and differential mortality (Egler 1954, Sutherland & Karlson 1977, Dean & Hurd 1980, Greene & Schoener 1982, Todd & Turner 1986, Turner & Todd 1994).

Bryozoans are often an important component in early community development, particularly at high latitudes (Moyano 1984, Lopez Gappa 1989, Rauschert 1991, Barnes 1995a,b). Chapters 2, 3 and 4 have shown that at the (Signy Island) sites studied, bryozoans are often the major occupiers of space on recently disturbed areas of rock faces and also on pebbles, rocks and small boulders. The abundance, variety and modular and encrusting structure of many bryozoans have made this taxon a very useful tool for examination of sublittoral developing community ecology (Moyano 1984, Rubin 1985, Lopez Gappa 1989, Todd & Turner 1989, Turner & Todd 1993).

This chapter investigates the level of community development over a 20 month period at sublittoral locations Signy Island (a latitude for which essentially nothing was known of settlement or recruitment). Such information allows important comparisons with

the contrasting results of studies involving artificial substrata in the high Antarctic and those of lower latitudes. The nature of the colonists, that is which species and broad groups predominated, was also a key area examined, particularly in comparison with the communities found on adjacent rocks and pebbles (previous chapter). The influence of depth and thus disturbance (and in particular ice scour) was investigated by positioning the plates over the depth range 6-25 m.

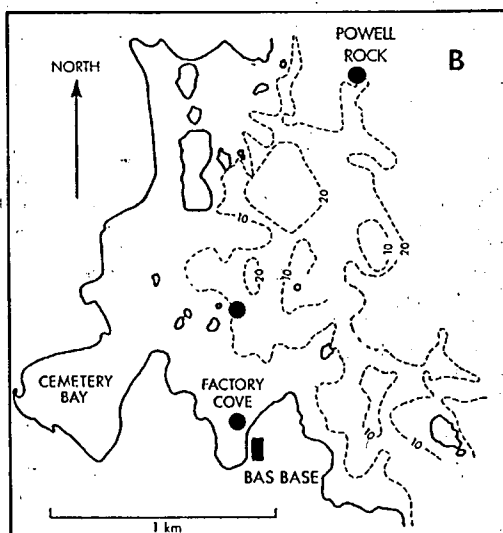
Materials and methods

Study sites

The study was undertaken at Factory Cove, Cam Rock and Powell Rock in Borge Bay, at three of the approximate locations used for studies of natural small scale substrata in the previous chapter. The position of these sites is illustrated in Fig 5.1. The substratum of small boulders and pebbles in a sand/mud matrix were similar between sites and the depths at mid tide were approximately 6 m, 12 m and 25 m respectively. Disturbance, primary productivity and light climate were highly seasonal, at all sites, as described for this location in the previous chapter and by Clarke *et al.* (1988) and Leakey *et al.* (1994). Sea or fast-ice cover tends to be longer the closer a given site is to land.

Figure 5.1

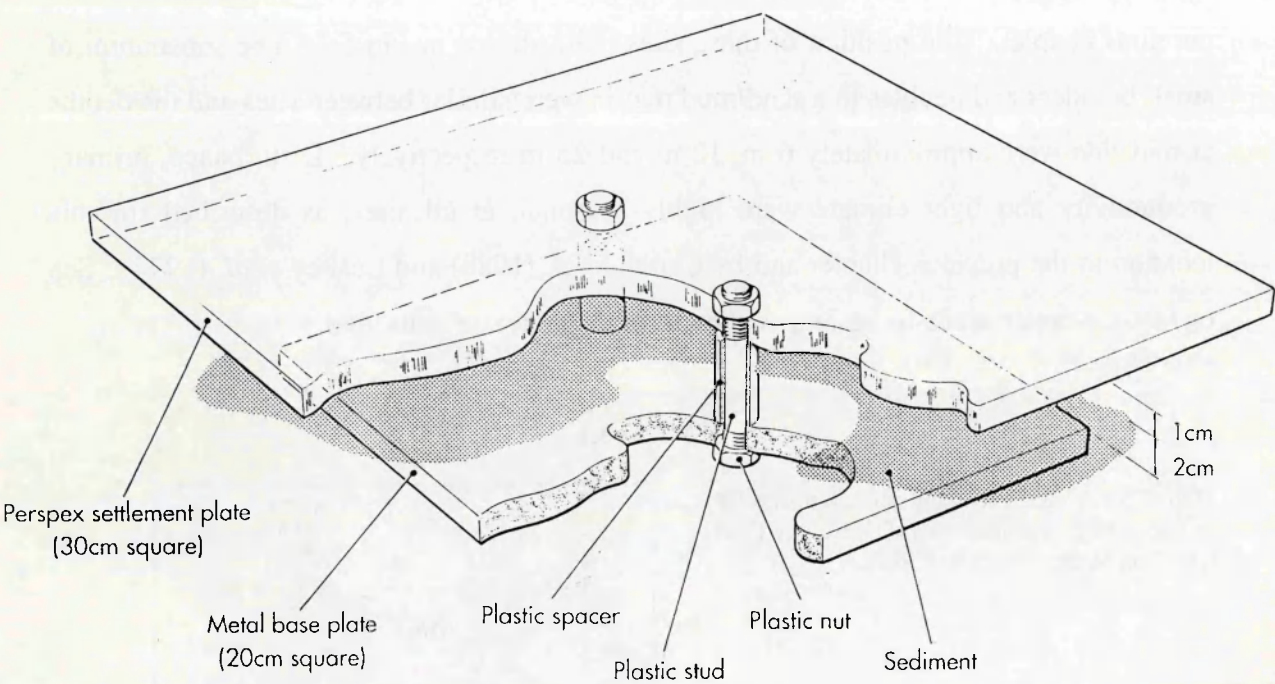
Map of Signy Island showing collection sites (●) in Borge Bay. Site labels are, FC: Factory Cove, CR: Cam Rock, PR: Powell Rock.



Settlement plate design and placement

The settlement plates were constructed of roughened clear perspex panels (30cm x 30cm x 1.2cm), each bolted horizontally above a metal panel of similar dimensions. Vertical separation was achieved by 3cm Perspex spacers, and the metal panel buried in substratum such that the bottom surface of the plates were 1 cm above the substratum (Fig. 5.2). The panels were attempting to simulate broadly the top and undersides of the boulders found at these sites.

Figure 5.2
Design of settlement plate, shown as positioned *in situ*



impact. The phenomenon of ice scour is a regular occurrence in Borge Bay and, as discussed in the first two chapters, has important influences on community development (see also Peck & Bullough 1993, Barnes 1995a,b). The influence of anchor ice has been shown to be a major factor in the development of sublittoral communities in high Arctic (Reimnitz *et al.* 1986) and Antarctic conditions (Dayton *et al.* 1970, Dayton 1989). At the lower latitudes of the Antarctic Peninsula (Rauschert 1986, 1991) and Signy Island (Barnes 1995a), however, anchor ice was rarely observed and consequently its influence on community development must be minor. Fast-ice covered the sea surface above these plates during the two winter periods (12.5 months total) of the 20 month experiment. The maximum area covered on any surface of the 6 m plates was less than 3% (Table 5.1).

Encrusting fauna dominated the area colonised on all surfaces of the plates situated at 12 m and algae were not present. Although the fauna was heavily dominated by spirorbids, one species of cyclostome and two species of cheilostome bryozoans were also present. No overgrowth of any recruits was observed. The maximum area covered on any surface was less than 5% and the upper surfaces had higher levels of coverage than the lower, similarly to those at 6 m (Table 5.1). None of these plates seemed to have been scoured or damaged by ice, although iceberg impact on substrata was noted in the vicinity of the experiment during the period the plates were immersed.

Table 5.1

Mean and maximum (in brackets) area colonisation by organisms of settlement plates deployed at three discrete depths over a 20 month period at Signy Island.

Depth (m)	N	Settlement plate surface covered (% total area)		
		Upper	Lower	Sides
6	5	0.72 (1.77)	1.25 (2.69)	0.71 (1.34)
12	4	0.19 (0.23)	2.41 (4.60)	1.09 (1.30)
25	4	6.54 (11.62)	4.71 (8.63)	7.49 (12.30)

Polychaetes (mostly spirorbids) represented the greatest number of recruitment events on all surfaces of the 25 m plates, and occupied the most area on the upper surface.

Early in the austral winter (July) of 1991, 4 plates were immersed at each of the two deeper locations and 5 at the 6 m location, using SCUBA. The plates were aligned horizontally and placed 1 metre apart from each other. They were retrieved 20 months later in 1993, and subsequently examined using a binocular microscope. All encrusting fauna was identified to the lowest taxonomic level possible and all colonies of clonal organisms counted. The total surface area occupied by every species (of bryozoan) on each surface was estimated by measuring the area of colonies with an image analyser. This technique has been shown to be one of the most accurate methods of per cent cover estimation (Meese & Tomich 1992). Similar methods were used for 6 smaller plates (5cm x 5cm x 0.3cm) immersed to 38 m at Outer Island, for 10 months (February 1992 - November 1992).

Artificial materials were used in preference to natural substrata as they confer a number of advantages in homogeneity. All the plates were of similar size, surface area, smoothness, and current resistance, allowing comparisons to be made between plates within and between depths. Studies involving terminal or long interval analysis, such as this, measure recruitment (the surviving colonies) rather than settlement (the total number of individuals that may have settled). The density of recruitment observed at all depths in this study suggested that subsequent larval settlement was probably not significantly affected by the space already occupied (see Connell 1985). As the plates were only handled once at the end of the experiment, the effects of handling were unconsidered but were probably low (see Todd & Turner 1988).

Results

The five plates in the shallowest location showed very low levels of colonisation, and the colonising organisms were predominantly encrusting algae. Polychaetes of the family spirorbidae were the only encrusting animals present, occurring mainly on the undersurface. Two of the plates had been completely scoured and broken into several pieces by iceberg

On the lower surface the area colonised by polychaetes (mostly other tubicoloid families rather than spirorbids) was similar to that occupied by bryozoans, and bryozoans dominated the sides of the plates. A total of two species of cyclostomes and 15 species of cheilostomes were present with a maximum of 209 colonies (0.23 colonies per cm²) occurring on the lower surface. The bryozoan species present or proportions of each species present varied little between the plates at this depth, although the maximum number of colonies, species and area colonised on each surface of a plate was more than double the minimum. Bryozoans overgrew spirorbids in all ten bryozoan-spirorbid interactions observed, whilst five bryozoan-bryozoan interactions were also recorded. Little iceberg activity was recorded in the vicinity of the plates and similarly to those at 12 m were thought to be untouched by ice. Sea-ice covered the sea surface above the plates for about 11.5 months. The maximum area colonised was less than 13% and, in contrast to the plates from shallower depths, the lower surface was colonised to a greater extent than the upper surface and the greatest level was found on the sides of the plates.

Figure 5.3

a. Mean percent area of settlement plates covered by colonising fauna at the three study depths. Settlement plate surfaces are ○ = Top, ● = Base, ◐ = sides.

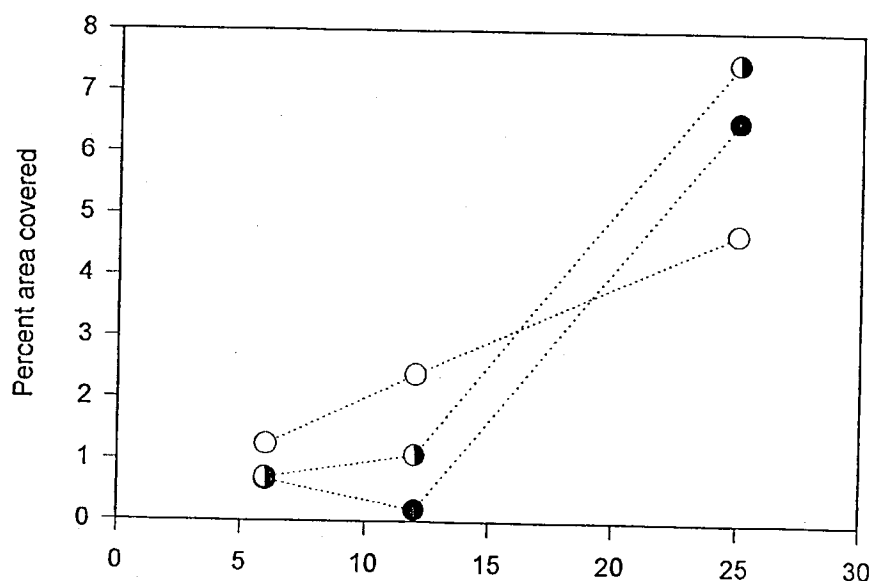
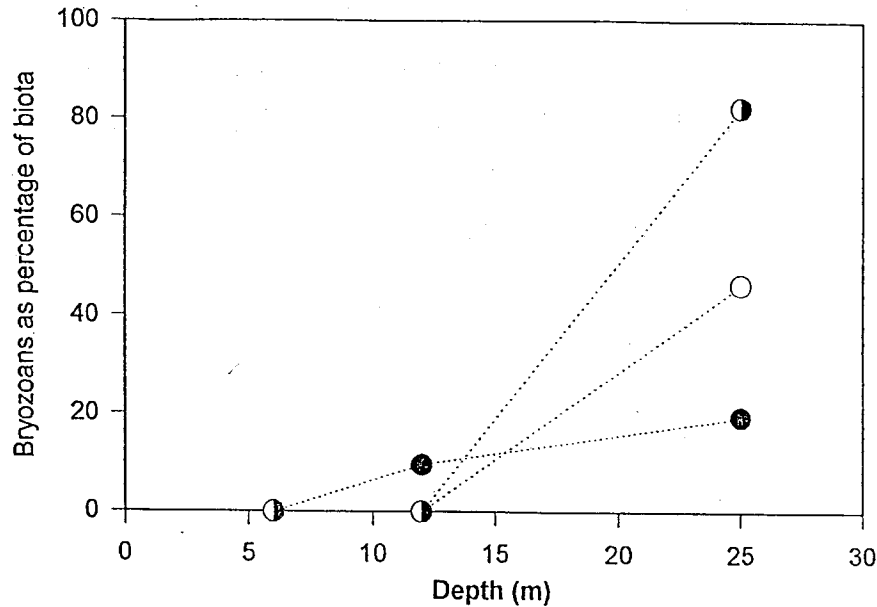


Figure 5.3

b. Bryozoan percentage of epibiota with settlement plate surface at the three study depths. Settlement plate surfaces are ○ = Top, ● = Base, ◐ = sides.



The smaller plates at 38 m, that had been immersed for just a 10 month period, were fixed to trays involved in another experiment and thus only the lower surfaces could be measured. A total of eight species were recorded and a maximum of 210 colonies or 8.4 colonies per cm², but the maximum area covered was below 12%. Spirorbids were present, but occupied only a minor proportion of the total area colonised on each plate.

Surface orientation and depth of the settlement plates deployed, were found to exert a variety of influences on recruitment. The degree of faunal colonisation increased with depth (Two way ANOVA $F=100.4$, $P<0.001$), although to a different extent on the upper surface from that on the lower or plate sides (Figure 5.3a). The greatest average degree of faunal colonisation occurred on the 38 m plates, but the different periods of immersion (10 versus 21 months) and smaller size meant that comparisons were not possible with the plates at shallower sites (see Jackson 1977). The pattern of overall colonisation with depth was similar on all surfaces, though increased at 5 m due to algal growth on the upper surface. The influence of surface orientation on the number of colonising spirorbids, with depth, was significantly different between surfaces (Figure 5.3b). This comparison was not possible with any other organisms, as spirorbids were the only taxon to be present on all panel surfaces and at all three depths. The abundances of the 15 species of cheilostome

bryozoans observed in the study are shown in Table 5.2 (for each surface of the plates recovered from 25 m). Three species, *Celleporella bougainvillei* (d'Orbigny), *Inversiula nutrix* Jullien (also both present on the plates recovered from 12 m) and *Celleporella antarctica* Moyano & Gordon, were particularly abundant, comprising over 55% of colonies and area occupied on the lower surface of the plates, over 70% on the sides of the plates and over 80% on the top surface.

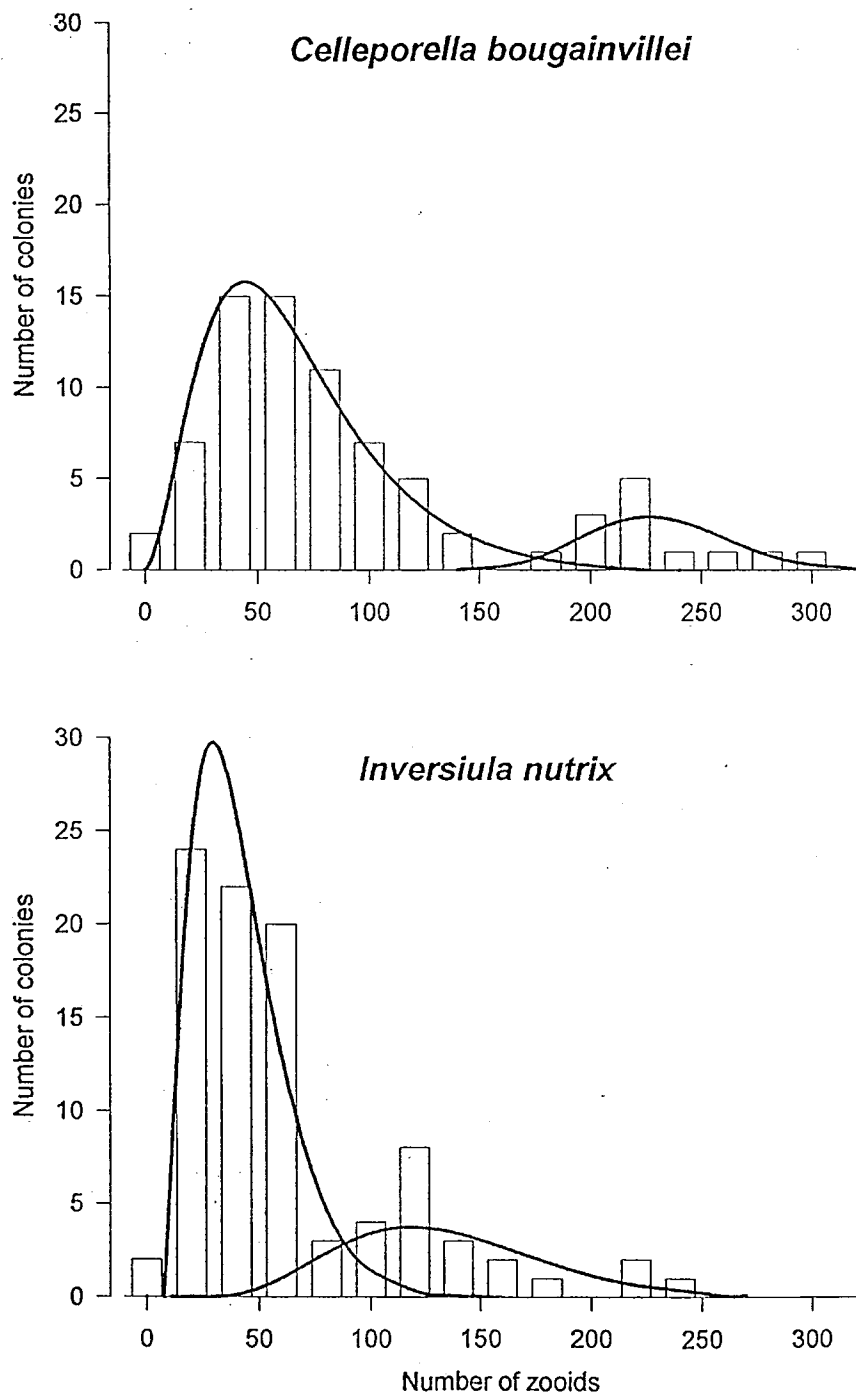
Table 5.2

Total abundance of 15 species of cheilostome bryozoans on settlement plates and 'background' rocks at 25 m. Frequency of occurrence is indicated by + (rare, mean <10 colonies per plate and on <10% rocks) ++ (occasional, 10 < mean <30 colonies per plate, and 10% < on rocks <50%) and +++ (abundant, mean >30 colonies per plate, and on >50% rocks).

Bryozoan species	Abundance on plates	Abundance on rocks
<i>Aimulosa antarctica</i>	+	++
<i>Amphiblestrum familiaris</i>	+	++
<i>Arachnopusia inchoata</i>	+	++
<i>Beania erecta</i>		+
<i>Celleporella antarctica</i>	+++	+
<i>Celleporella bougainvillei</i>	+++	+++
<i>Celleporella dictyota</i>	++	+
<i>Ellisina antarctica</i>	+	+++
<i>Escharoides tridens</i>	++	+++
<i>Fenestrulina rugula</i>	+	+
<i>Harpecia spinosissima</i>	+	+
<i>Hippadanella inerma</i>	+	+
<i>Inversiula nutrix</i>	+++	+++
<i>Klugarella antarctica</i>		++
<i>Lacerna eatoni</i>	+	++
<i>Lageneschara lyrullata</i>		+
<i>Micropora brevissima</i>	+++	+++
<i>Microporella stenopora</i>	+	++
<i>Smittina</i> sp.		+
<i>Smittina rogickae</i>		+++
<i>Valdemunitella lata</i>		+

Figure 5.4

Histogram with fitted models (using MIX software) of the colony size (in numbers of zooids) distributions of the two most abundant bryozoan species occurring on the 25 m settlement plates. The fitted curves illustrate the probable explanation for the data in terms of two separate recruitment events of differing magnitude in a. *Celleporella bougainvillei* and b. *Inversiula nutrix*.



Analysis of the number of zooids per colony of *Inversiula nutrix* and *Celleporella bougainvillei* (the only species for which sufficient data were available) suggests the possibility that there were two peaks of recruitment during the period the plates were deployed (Figure 5.4a & b). It is likely the left hand peak represents recruitment in late 1992 or early 1993 and the right hand peak recruitment in 1991/1992. If this interpretation is correct, the data may illustrate annual variations in recruitment (for these two species at least) as recorded by many long term studies with artificial substrata (Coe & Allen 1937, Loosanoff 1964, 1966, Sutherland & Karlson 1977, Todd & Turner 1986). High mortality after each settlement event however, either through short lived adults, predation or physical effects as observed in a number of similar though temperate studies (Sutherland & Karlson, 1977, Osman 1982, Turner & Todd 1993), might also explain the distribution of data. Bryozoan mortality is an unlikely explanation though, as most damaged or dead colonies would remain and be detected on the plate surfaces, yet appeared to constitute only $\approx 5\%$ of colonies in *Inversiula nutrix* and *Celleporella bougainvillei*. Overgrowth of colonies was negligible, but the explanation of recruitment variation does assume that there is not a large mortality involving complete removal of discrete colonies.

Discussion

Studies with immersed settlement plates or other artificial substrata at most latitudes have shown approximately comparable levels of colonisation (percentage cover) within 1 year: Jamaica, over 80% (Jackson 1977), U.K., over 80% (Withers & Thorp 1977, Todd & Turner 1989), South Africa, 100% (Barkai & Branch 1988) and Patagonia, approximately 75% in 9 months (Lopez Gappa 1989). Colonisation of the plates deployed at all three depths at Signy Island was over an order of magnitude less, after two years of immersion. A similar long term settlement plate study carried out at King George Island, South Shetlands, also in the maritime Antarctic, resulted in most of the plates being lost because of ice, but the remainder being richly colonised after 3 years (Rauschert 1991). The only study involving artificial substrata that has been carried out to date in the high Antarctic (McMurdo Sound) showed virtually no colonisation for 5 years but then a high degree of

colonisation within the next 4 years (Dayton 1989). The low degree of initial colonisation, inter annual variations in recruitment and the relatively few taxonomic groups involved in colonisation are important similarities found between this study and that by Dayton (1989).

Although better post-settlement survival has been documented in panels immersed for longer periods (Scheer 1945, Dean & Hurd 1980, Chalmer 1982, Turner & Todd 1993), the level of mortality (e.g., <5% for *Inversiula nutrix*) in recruits at Signy Island was very low in comparison with other community studies on artificial substrata carried out over similar periods (e.g. Todd & Turner 1991, Turner & Todd 1994). A number of factors may have been responsible for the apparent low mortality after recruitment. As the level of colonisation on the plates was low, density dependant inhibition of settlement by post-larval forms (Connel & Slatyer 1977, Grosberg 1981) would have been correspondingly low. Food would be super abundant if recruitment mainly took place during the intense summer phytoplankton bloom (Whitaker 1982, Clarke *et al.* 1988, Leakey *et al.* 1994) and the level of predation on most 'background' species appeared low (see chapter 11). Occasional catastrophic destruction of entire communities by ice scour, as occurred to two of the 6 m panels in this study, probably represents an important fraction of total mortality.

In most studies of colonisation polychaetes and bryozoans have been found to be responsible for most of the initial colonisation (Goren 1979, Kay & Keough 1981, Rubin 1985, Lopez Gappa 1989, Todd & Turner 1986, 1989). In this study observation using SCUBA indicated that polychaetes (spirorbids) were the first animal taxon to colonise the plates at all depths, and only at 25 m did bryozoans occupy more area after 21 months. Polychaetes and bryozoans were also observed to be the predominant colonisers of more ephemeral or regularly disturbed substrata such as pebbles and rocks in the sublittoral at Signy Island (chapter 4). On more stable substrata, such as rock faces, bryozoans have occasionally been found to dominate the entire encrusting biota in shallower or recently disturbed areas (Barnes 1995a,b). Community development is usually greater on the lower surfaces of settlement plates (Pomerat & Reiner 1942, McDougall 1943, Harriott & Fisk 1987). The number of bryozoan species, colonies and area occupied was greater on the lower surface at 25 m, but greater on the upper surface at 12 m. Recruitment of spirorbids

however, was much greater on the upper surface at 12 and 25 m, and recruitment remained approximately constant with depth on the lower surface and sides (Figure 5.3b).

The community development, particularly with respect to bryozoans, can be compared with the natural or 'background' communities on pebbles and rocks in the immediate vicinity. A number of encrusting bryozoan species occurred on rocks at 5 m, despite the lack of colonisation on the plates. There were, however, fewer species and these were less abundant than those on rocks at 12 m, and these communities were in turn less dense and species rich than those at 25 m (Chapter 4). Variations in supply of potentially colonising larvae (greater abundance of species and colonies with depth leads possibly to a greater supply of larvae) may at least partly explain the observed differences in recruitment with depth. The frequency and influence of ice impact in the shallow sublittoral at Signy Island (see Peck & Bullough 1993, Barnes & Clarke 1994, Barnes 1995a, b) probably inhibits community development to such an extent that a 'climax community' is an irrelevant concept for settlement panels immersed at 6 m in Borge Bay, as described for much of the shallow boreal sublittoral (Field 1982). The bryozoan community of the plates at 25 m resembled the 'background' community most closely in terms of species (Table 5.2 - using data from chapter 4). The most abundant species on the plates at 25 m (and the only species on the plates at 12 m) were those characterised by high dispersal and fast growth but of poor overgrowth competitive strength (chapter 4). A similar pattern was observed on settlement plates retrieved from 40 m in the high Antarctic (Moyano 1984). Of the six species present on background rocks but not the settlement plates, five were characterised by low abundance and slow growth, but good overgrowth competitors with other bryozoans, and in one case was only found growing on top of other bryozoans (see chapter 4). This study suggested an orderly succession, observable at both the levels of species and phyla, whereby early colonisers facilitated settlement for later arrivals (see Scheer 1945, Connell & Slatyer 1977). In contrast there was little evidence that ultimately dominant forms were present from the outset, with the potential of later expression through slower growth rates (Egler 1954, Chalmer 1982, Turner & Todd 1994). The complexity of seasonal variations in recruitment, growth and mortality have been suggested by studies of community development on artificial substrata,

as reasons for deviation from 'classical' succession. This complexity however may be reduced at Signy Island and polar environs in general, by the extreme seasonality of the environment (Clarke *et al.* 1988, Clarke 1988) and the frequency of disturbance limiting community development (Peck & Bullough 1993, Barnes 1995a,b).

The pattern of early community development described in this chapter combined with the observations in previous chapters on encrusting hard substratum community dynamics at Signy Island, suggests a greater similarity to classical succession theory (Clements 1916, McCormick 1968, Odum 1969, Drury & Nisbet 1973) than has been reported from studies at lower latitudes (Sutherland & Karlson 1977, Dean & Hurd 1980, Breitburg 1985, Turner & Todd 1994).

Plate 2

A clump of the brachiopod *Liothyrella uva* encrusted by epibiotic bryozoans.



Colonisation of biotic substrata: some common macroinvertebrates

Introduction

Earlier chapters of this thesis have discussed the presence of large, predominantly sessile, benthic communities (Belyaev & Ushakov, 1957; Tressler, 1964; Knox, 1970; Galéron *et al.*, 1992) and that such assemblages may occur as shallow as the sublittoral at Signy Island (White & Robins, 1972; Barnes, 1995a,b). In such dense sessile communities, space may be a limiting resource (Dayton, 1971; Paine, 1974; Jackson, 1977; Doherty, 1979) and other taxa may often be used as substrata. This is particularly true of sessile forms with hard external shells, such as brachiopods (Doherty, 1979; Hammond, 1984; Witman & Suchanek, 1984; Thayer & Allmon, 1990). Such epibiota may benefit from higher levels of survivorship and recruitment (Lohse, 1993) or feeding (Laihonen & Furman, 1986) compared with those on nearby abiotic substrata. Epibiota have been shown to have a wide range of impacts on the substratum organisms, ranging from beneficial (Bloom, 1975), through negligible (Seed & O'Connor, 1981) to adverse effects. The latter may occur through altering feeding and respiration (Thayer & Allmon, 1990; Allen *et al.*, 1993), reproduction (Willey *et al.*, 1990) or survival (Witman & Suchanek, 1984; Thayer & Allmon, 1990; Willey *et al.*, 1990; Weissman *et al.*, 1993; Buckley & Ebersole, 1994).

Bryozoans are a common, and often the most abundant, faunal component of epibiota on a wide range of organism substrata, including algae (Stebbing, 1972), serpulid worm tubes (Rubin, 1985), corals (Jackson, 1979), mussels (Witman & Suchanek, 1984) and even the cephalopod *Nautilus* (Landman *et al.*, 1987) and sea turtles (Frazier *et al.*, 1992). Two common organisms in the local neashore marine environment at Signy Island that frequently bear epibiotic communities are the brachiopod *Liothyrella uva* Broderip and the limpet *Nacella concinna* Strebel. These two species are particularly suitable for study as they are both abundant over a similar range of depths in Borge Bay and were collected periodically as part of separate studies by other researchers. Whilst *Liothyrella* occurs predominantly in cryptic habitats, such as crevices, *Nacella* frequents exposed rock surface which represents an important ecological difference with respect to settlement by epibiota.

This chapter discusses which taxa were the dominant epibiota on the common shallow-water macroinvertebrates at Signy Island and how the epibiotic communities varied with the nature and size of substratum organism, and with depth. The epibiotic communities found were compared with the fouling communities of nearby surrounding non-biotic substrata at similar depths (see chapter 4). The interactions of the various organism components of the epibiota were also examined, along with their interactions with, or effect on, the substratum organism.

Materials and methods

Study site and species

Specimens for this study were collected from several locations around Borge Bay, including Shallow Bay, Factory Cove, Bare Rock, Polynesia Point, Powell Rock and Outer Island (see chapters 2, 3 and 4 for maps). The main study concentrated on epibiota of the brachiopod *Liothyrella uva* and the Antarctic limpet *Nacella concinna*, both of which are locally abundant (Picken, 1980). In addition, representatives of other important local taxa were also examined for epibiota; these included the octocoral *Ascolepis* sp., the isopod *Glyptonotus antarcticus* Eights and various ascidians, holothurians and pycnogonids.

Collection and measurement

A total of 400 brachiopods were collected using SCUBA from depths of 6m, 12m and 19m, during the austral summers of 1991/1992 and 1992/1993. 974 limpets were collected from these same three locations, plus 323 more from two other locations, one intertidal and one at 25m. The other taxa were only collected where found abundantly: holothurians at 6 and 19m, pycnogonids from 6 m, *Ascolepis* at 6m, and *Glyptonotus* at 12m. The ascidians were collected from 50m by trawling, further offshore, as part of a general benthic faunal survey (chapter 3).

The lengths of the brachiopods and limpets were measured with vernier callipers. The surface area of the shell of brachiopods and limpets was measured using a thin, non-elastic, net marked in square centimetres. This method was also used for determining the area of the shell covered by each taxon of epibiota. For *Ascolepis* and *Glyptonotus*, only length was measured, as their complex shape meant that area measurements could not be made precisely. For all individual substratum organisms the number of colonies of each epibiotic bryozoan species was recorded, thus producing total numbers of both species and colonies. A binocular microscope suspended over a water-bath, held at ambient seawater temperature, was used in identification, so specimens could be either returned to the sea or used for other experiments.

Results

Epibiota on *Liothyrella uva*

At all three depths sampled, epibiota were found to be present on few of the individuals of smallest valve size but were present on all of largest valve size (Table 6.1). The total proportion of valve area covered by epibiota increased from below 20%, in the smallest size classes, to over 55% for the largest, (Fig. 6.1a). The rate of increase of coverage with valve size was similar at each of the three depths, but the brachiopods from 6m, of every size grouping, had a significantly greater percentage cover of epibiota (ANOVA $p < 0.001$) than those from deeper locations. Epibiotic coverage, with valve size, was similar for brachiopods from 12m and 19m (Fig. 6.1a).

Juvenile or larval brachiopods appear to settle preferentially on adult brachiopods of the same species, occasionally leading to clumps of epibiotic individuals (L.S.Peck, pers. comm.1994). It was possible that the epibiotic colonisation of clumped and solitary brachiopods might differ. Although a significant difference (ANOVA, $F=221$, $P < 0.01$) was noted in the number of colonies of epibiota on clumped and solitary shells at 6 metres, this only accounted for less than 2% of the total variation. At 12 metres, the other depth for

which data were available, clumped brachiopods did not carry significantly different numbers of epibiotic colonies. A comparison of the total areas of valve covered showed no significant difference in coverage between clumped and solitary animals (Multiple regression, t value = 0.29, $P > 0.05$).

The three main colonising phyla of epibiota on *Liothyrella* were bryozoans, annelids (polychaetes) and sponges. Other minor colonisers (in terms of area covered) included entoprocts, cnidarians, ascidians and young *Liothyrella*. Coralline alga (probably *Lithothamnion*), which is one of the dominant area occupiers of much hard substratum in these localities (Chapter 2 & 3), was not as prevalent on *Liothyrella* shells (brachiopods tend to live in caves and crevices which limits light for algal photosynthesis). The proportions of the three main colonising taxa on brachiopods changed with shell size, and in a similar way at all three depths (example shown for 19m, Fig. 6.1b). The percentage of bryozoans increased with shell size from below 40% on the smallest hosts to over 90% of the epibiota on the largest shells. Polychaetes decreased in an inverse pattern to the bryozoans, whilst sponges varied only a little around 5% of the epibiota.

Table 6.1

Prevalence or percentage of shells carrying epibiota and total number of epibiotic bryozoan species on valves of *Liothyrella*, with valve length and sample depth. Total number of shells examined was 400, with between 12 and 48 per depth/size class.

Depth (m)	Shell length (mm)				
	0-15	15-25	25-35	35-45	45+
	Prevalence (percentage of shells bearing epibiota)				
6	30	21	3	100	100
12	0	25	73	100	100
18	18	71	100	96	100
	Total number of epibiotic bryozoan species				
6	1	2	5	12	11
12	0	1	4	11	12
18	1	3	8	13	13

Figure 6.1a

Relationship between area of valves of the brachiopod *Liothyrella uva* covered by epibiota and valve size. Data are shown as mean with SE, and plotted separately for 6 m (●), 12 m (◐) and 19 m (○) depth. Note displacement of vertical axis for clarity.

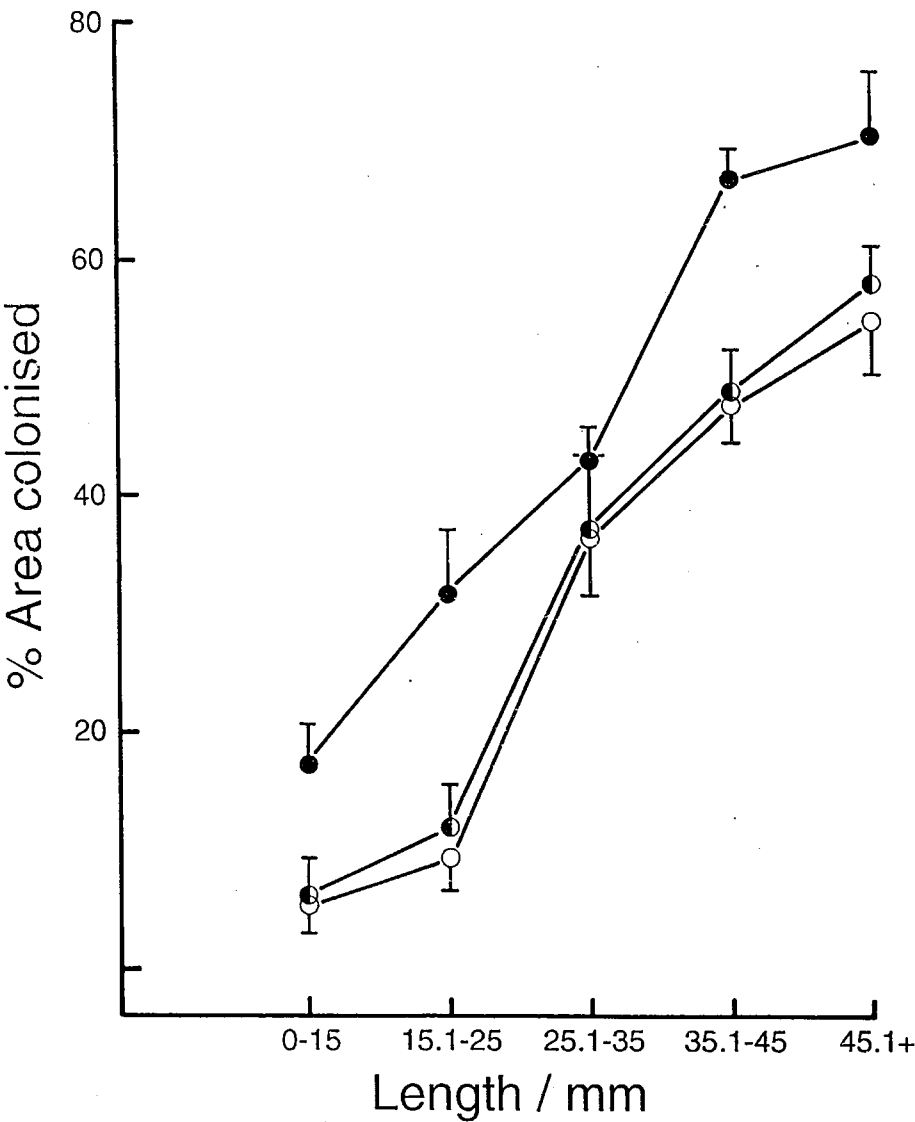
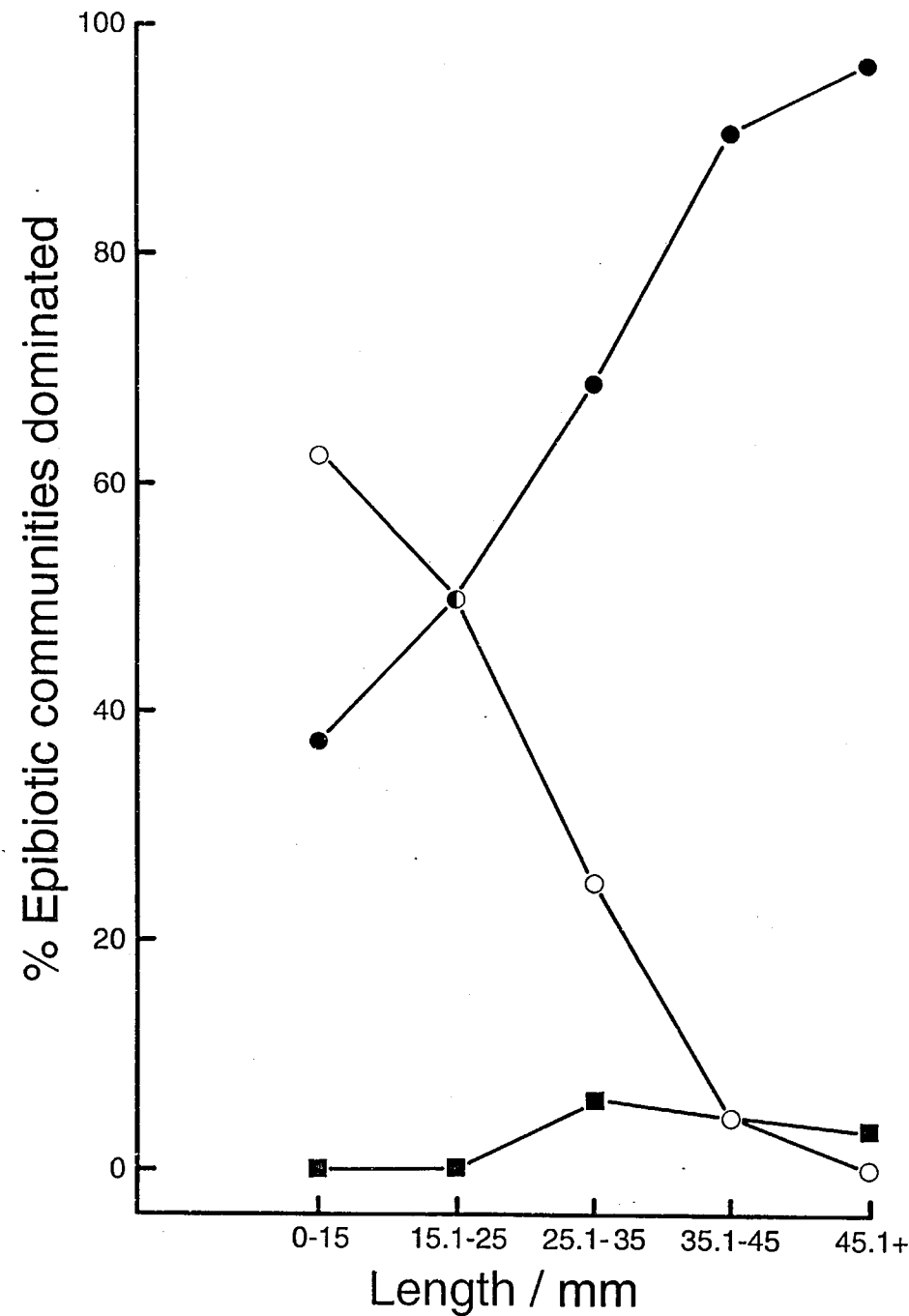


Figure 6.1b

Percentage of *Liothyrella* individuals dominated by each epibiotic taxon (at 19 metres). The phyla are Bryozoa (●), Annelida (○) and Porifera (■). Note displacement of the vertical axis for clarity.



The number of bryozoan species occurring on *Liothyrella*, increased with shell size, but not greatly with depth (Table 6.1). In fact, most of the dominant epifaunal bryozoan species were similar, in terms of mean colony density and prevalence on *Liothyrella*, at each depth; they were also in similar proportion to one another (Table 6.2).

Table 6.2

Mean colony density (number of colonies per cm²) and occurrence (percentage of shells bearing a given species) of cheilostome bryozoans on the brachiopod *Liothyrella uva*, at three depth locations. Species are ranked according to occurrence at 19 m (see table 6.4).

Species	Density			Occurrence		
	6 m	12 m	19 m	6 m	12 m	19 m
<i>Celleporella antarctica</i>	1.65	0.44	1.18	77.9	45.3	64.9
<i>Micropora brevissima</i>	0.06	0.06	0.22	10.3	10.9	33.6
<i>Klugarella antarctica</i>	0.04	0.06	0.13	5.1	10.2	26.1
<i>Arachnopusia inchoata</i>	0.04	0.03	0.10	11.0	11.7	24.6
<i>Lacerna eatoni</i>	0.02	0.04	0.07	4.4	10.9	17.9
<i>Ellisina antarctica</i>	0.11	0.03	0.06	21.3	6.3	13.4
<i>Amphiblestrum familiaris</i>	0.03	0.07	0.06	6.6	13.3	11.9
<i>Xylochoiridens rangifer</i>	0.19	0.11	0.04	24.3	21.1	11.1
<i>Beania erecta</i>	0.36	0.32	0.04	23.5	28.9	6.0
Other species	0.04	0.03	0.07	6.6	6.2	12.7

A number of significant associations were found between the occurrence of bryozoan epizoic species (Chi square, $P<0.01$), particularly in a group of 5 species occurring commonly on specimens of *Liothyrella* at all three depths (Fig. 6.2). The strongest correlations, in both occurrence and abundance, of these 5 species, were those which involved *Micropora brevissima*. Associations between the other four species in this group were likely to be simply a product of their each being independently associated with *Micropora*, and as a result often occurring together (Fig. 6.2). Another association, probably independent from the *Micropora* complex, was that between *Beania erecta* and

Xylochotridens rangifer Hayward & Thorpe. At 6 and 12 m there was a strong positive association of occurrence between the two species, but weak with respect to abundance, and there was no association at all at 19 m, despite both species being present (Fig. 6.2).

A total of 61 interactions were noted involving sponges and bryozoans growing on the same *Liothyrella* shells. In most cases, it was difficult to tell whether the sponge had settled directly onto a bryozoan colony and subsequently suffocated the underlying colony through faster growth, or had overgrown a bryozoan colony after contact between growth margins. Either way, sponges overgrew bryozoans (whatever species) on all 61 of these recorded interactions. Bryozoans overgrew the tubes of spirorbid worms, though spirorbids frequently also settled on top of bryozoan colonies. Unfortunately time constraints precluded a full analysis of bryozoan-spirorbid interactions.

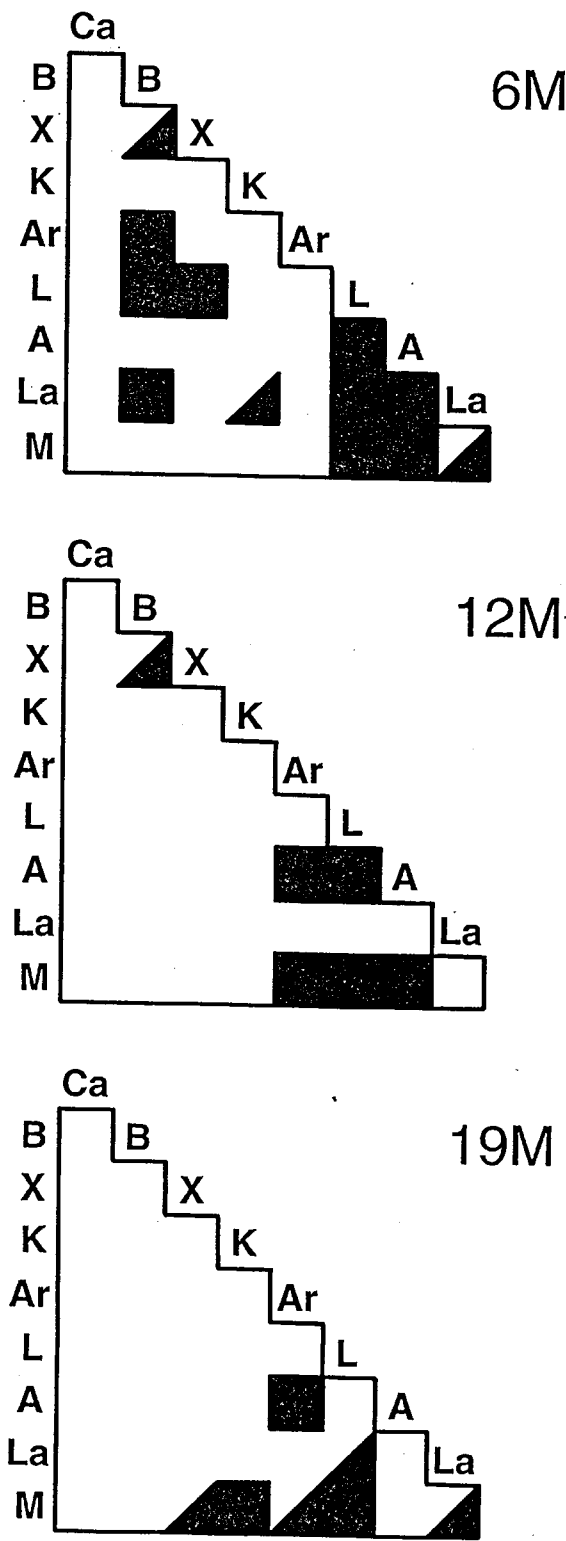
On some individual *Liothyrella* dense growth of bryozoan epibiota appeared to have caused mortality of the brachiopod. On twelve observed occasions, up to ten young brachiopods which had settled on an adult *Liothyrella* shell, were smothered by *Arachnopusia inchoata* Hayward & Thorpe or *Beania erecta* also growing on the adult. In four adult brachiopods the encrusting bryozoan *Arachnopusia inchoata* was found to have blocked the gape, thereby restricting the feeding and respiratory activity. The bryozoans had grown over both valves, and were possibly responsible for death. Many *Liothyrella* individuals were, however, able to maintain gape despite total, or near total, epifaunal cover; a similar observation was made by Thayer (1975).

Epibiota on *Nacella concinna*

The limpet *Nacella concinna* differs from the brachiopod *Liothyrella uva* as a substratum for epibiota in being a vagile animal. Also, in contrast to the brachiopod, *Nacella* populations occur principally on open regions (such as boulder fields) (Picken, 1980) where light penetration allows growth of its algal food matter as well as potential epifaunal algae on the limpet shell. This has implications for which taxa predominate epibiotically as well as the possibility of increased disturbance levels from water movement.

Figure 6.2

Associations between different epibiotic bryozoan species on *Liothyrella* valves. Blocking of the top left of each box shows significant ($P<0.01$) correlation of abundance, and blocking of the bottom right shows significant correlation in percentage occurrence. Data are shown separately for 6m, 12 m and 19 m. The species abbreviations are : B *Beania erecta*, X *Xylochotridens rangifer*, K *Klugarella antarctica*, Ar *Arachnopusia inchoata*, L *Ellisina antarctica*, A *Amphiblestrum familiaris*, La *Lacerna eatoni*, M *Micropora brevissima*, Ca *Celleporella antarctica*.



Probably a more important disturbance factor, and of greatest effect to newly settled colonising epibiota, is the grazing of limpet shells by other limpets (Nolan, 1991).

In *Nacella* the proportion of shell colonised increased with both shell size and water depth (Fig. 6.3a). The highest proportions of the shell covered by epibiota (over 20% at the smallest size class increasing to over 60% at the largest size class) were similar to those of *Liothyrella*, although the mean values of cover at each depth vary more with depth than in *Liothyrella*. Also differing from the epibiota of *Liothyrella*, the mean values of epibiotic shell cover diverged between depths with increasing shell size. Probably the most striking difference between the shell epibiota of *Nacella* and *Liothyrella*, however, was that, in *Nacella*, shell coverage increased with depth for every size range, compared with the decrease with depth seen in *Liothyrella*.

As with *Liothyrella*, bryozoans and spirorbids were important space occupiers on the shell surface of limpets. In contrast to the eight epibiotic taxa on brachiopods, these were the only animal taxa represented on limpet shells. Limpets, like many hard surfaces at these depths that are not light shaded, carried an epibiota dominated by the coralline alga *Lithothamnion* (Fig. 6.3b). Only the largest limpets at the deepest of the three locations (19 m) had a shell epibiota dominated by animal taxa (bryozoans). Both the polychaetes and bryozoans occupied a much smaller overall proportion of the epibiota than on *Liothyrella*. This applied particularly to the spirorbids which reached a maximum of 15% of the epibiota compared with 63% of the epibiota on *Liothyrella*.

The epibiota of *Nacella* shells revealed a complex interaction between coralline algae and bryozoans. *Lithothamnion* overgrew bryozoan colonies whenever the two organisms met. Bryozoan colonies, however, frequently settled on top of *Lithothamnion*. Occasionally this resulted in a layered effect: after *Lithothamnion* had overgrown a bryozoan colony, a bryozoan settled on top of the algal overgrowth, which was then overgrown in turn by further *Lithothamnion*. Bryozoans became more competitive with depth, such that at the deepest location (25 m) the eventual outcome (seen in the largest shells) resulted in bryozoans occupying more area than the coralline alga. The change in

dominance with depth may partly be due to the diminishing light reaching the coralline algae, but also to a significant increase in bryozoan settlement. The number of bryozoan species occurring on limpet shells increased with depth and shell length, as did the number of colonies per shell (Table 6.3).

Figure 6.3a

Relationship between area of shells of the limpet *Nacella concinna* covered by epibiota and shell length. Data are shown as mean with SE, and plotted separately for 6 m (●), 12 m (◐) and 19 m (○). Note displacement of vertical axis for clarity.

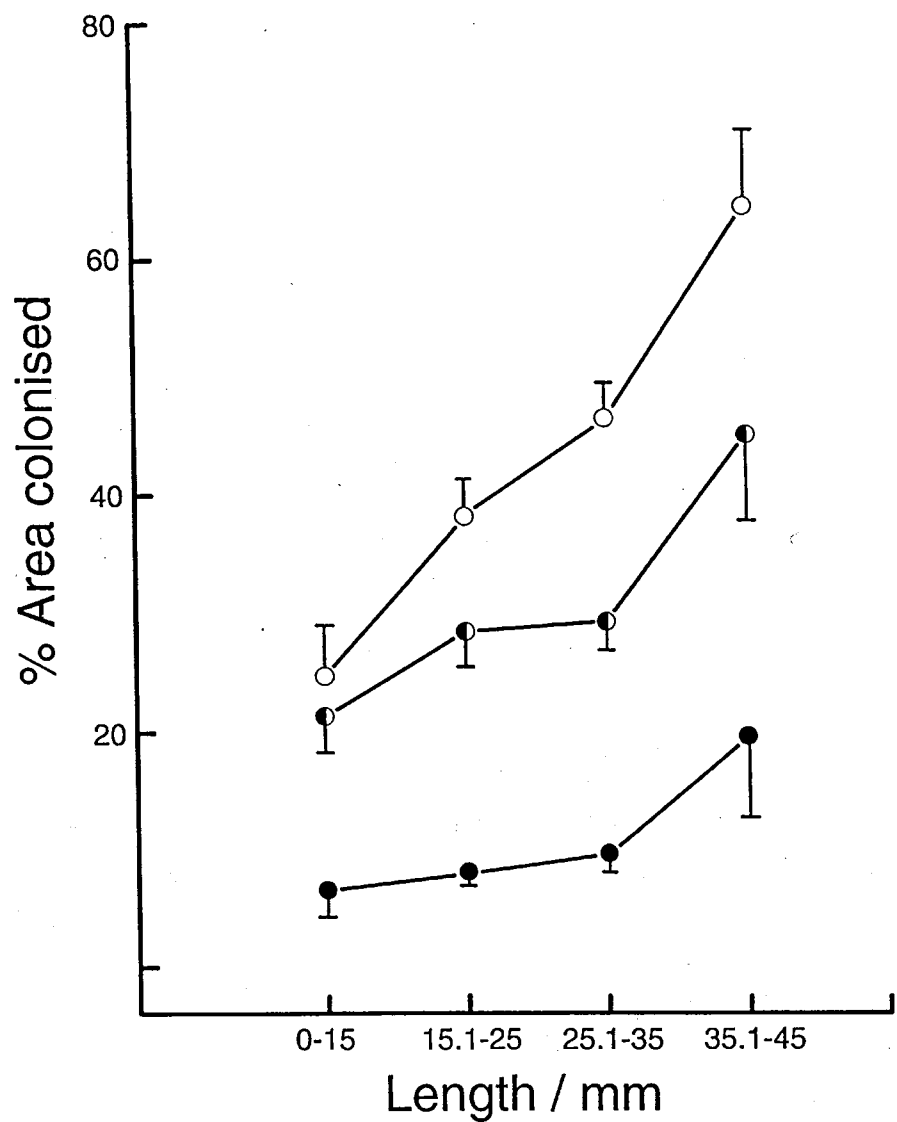


Figure 6.3b

Percentage of *Nacella* individuals dominated by each epibiotic taxon (at 19 m). The taxa are Bryozoa (●), Annelida (○) and the coralline alga *Lithothamnion* (Δ). Note displacement of the vertical axis for clarity.

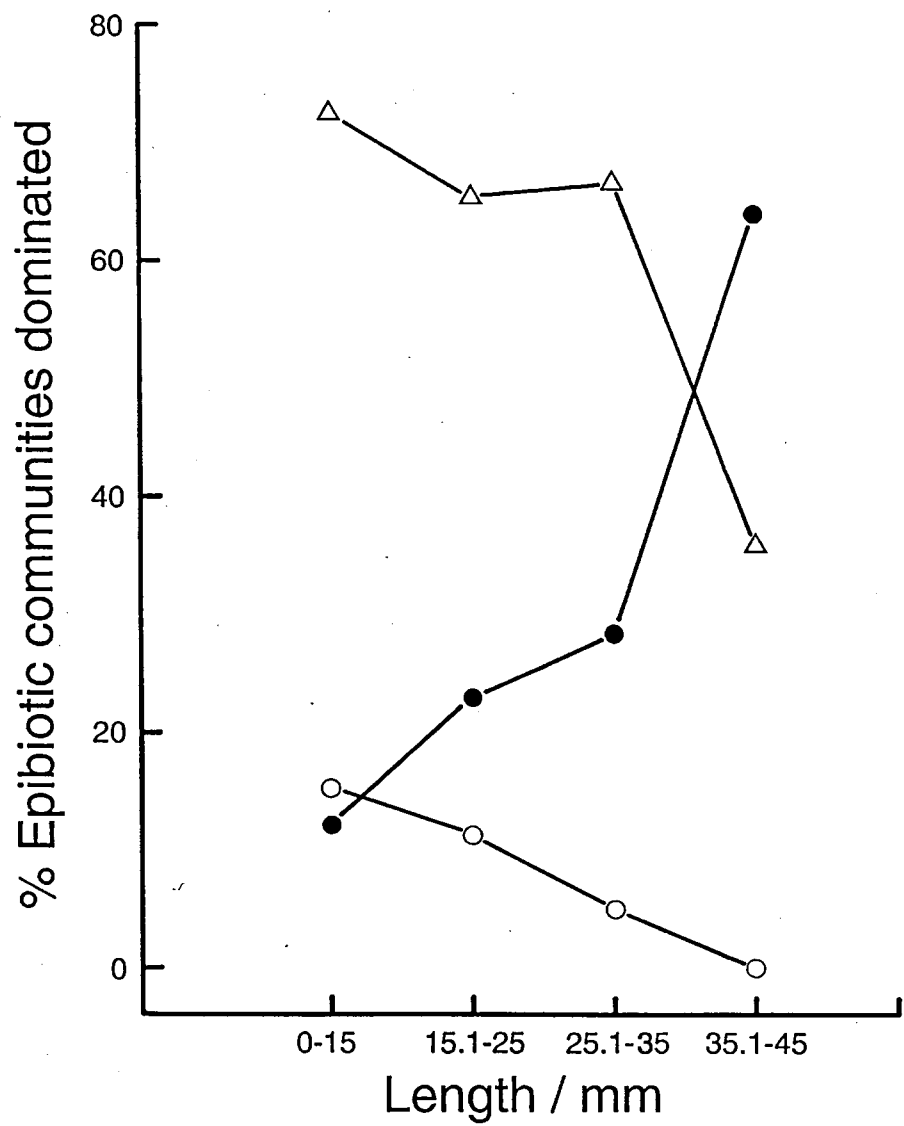


Table 6.3

Mean number of bryozoan colonies per shell, percentage of shells colonised by epifaunal bryozoans and total number of bryozoan species recorded at each depth, with shell length of *Nacella* and depth location.

Depth (m)	No of colonies per shell				% Shells colonised				Total no of bryozoan species
	Shell length (mm)								
	0-15	15-25	25-35	35+	0-15	15-25	25-35	35+	
6	0	0	0	1.1	0	0	1.0	21.4	1
12	0.6	1.1	1.8	2.8	42.2	57.4	59.7	85.7	5
19	0.4	1.4	1.9	4.9	33.3	70.4	61.3	85.7	5
25	0.9	2.5	3.7	7.4	50	84.2	92.3	100	11

Table 6.4

Percentage of shells bearing epibiotic bryozoan species (occurrence) at three depth locations, in the limpet *Nacella concinna*. Species ranked according to occurrence at 19 m.

Species	Occurrence			
	6 m	12 m	19 m	25 m
<i>Celleporella bougainvillei</i>	2.2	55.7	59.6	77.3
<i>Celleporella antarctica</i>	0	1.1	0.6	10.1
<i>Ellisina antarctica</i>	0	0.5	1.2	6.7
<i>Inversiula nutrix</i>	0	0	2.4	5.0
<i>Arachnopusia inchoata</i>	0	0.5	0	4.2
<i>Micropora brevissima</i>	0	0	0.6	2.5
Other species	0	0.5	0.6	6.7

The species composition of the epibiota on limpets was similar across all depth locations. One bryozoan species, *Celleporella bougainvillei* (d’Orbigny), greatly dominated the epibiotic community (Table 6.4). The bryozoan species composition and dominance on *Nacella* was very different from that of *Liothyrella*, despite the two epibiotic communities sharing a number of species in common. *Celleporella bougainvillei* occurred rarely on *Liothyrella*, whereas *Celleporella antarctica* Moyano & Gordon, which dominated

the occurrences on *Liothyrella*, occurred only rarely on *Nacella*. *Liothyrella* was host to a greater number of species, including some (such as *Xylochoiridens rangifer*) which were very rare on the surrounding hard substrata (chapter 4), whilst the bryozoans found in the epibiota of *Nacella* shells were all locally abundant species (Table 6.5).

Table 6.5

Frequency of occurrence (percentage of substrata bearing a given species) of some bryozoan species on shells of the brachiopod *Liothyrella*, rocks of similar size to *Liothyrella*, and rocks of all sizes (1cm² - 1000cm²) here termed Bkgnd ≈ background). Data are presented as percentages of all occurrences for each depth and substratum.

Species	% Frequency of occurrence on substratum								
	6m			12m (Depth)			19m (Depth)		
	Shell	Rocks	Bkgnd	Shell	Rocks	Bkgnd	Shell	Rocks	Bkgnd
<i>Celleporella antarctica</i>	77.9	0	1.9	45.3	0	0.6	64.9	0	6.5
<i>Beania erecta</i>	23.5	0	1.9	28.9	0	5.1	6.0	1.3	9.7
<i>Xylochoiridens rangifer</i>	24.3	0	0	21.1	0	0	11.1	0	0
<i>Klugarella antarctica</i>	5.1	0	0	10.2	0	0	26.1	3.9	17.5
<i>Micropora brevissima</i>	10.3	0	2.5	10.9	8.3	21.2	33.6	75	85.7
<i>Inversiula nutrix</i>	0	12.5	42.1	0	33.3	58.3	2.2	76.3	81.2
<i>Celleporella bougainvillei</i>	2.3	20	47.8	2.4	16.7	35.9	5.2	12.3	46.1
<i>Arachnopusia inchoata</i>	11.0	0	3.8	11.7	1.7	19.2	24.6	7.1	31.8
Total Number of bryozoan species recorded	12	2	10	12	6	12	16	14	16

Epibiota on other locally common species

A range of other substratum organisms common in shallow water in Borge Bay also carried epibiota. These included the octocoral *Ascolepis* sp., the isopod *Glyptonotus antarcticus*, the holothurian *Psolus charcoti*, and a variety of pycnogonids and ascidians. These all had encrusting epibiota dominated by bryozoans (Table 6.6). The epibiota of these groups occupied only a small proportion of the available area for each animal (≈<10%), and, with the exception of the ascidians, were composed of many fewer species than on *Liothyrella*. Of the other locally common macroinvertebrates in Borge Bay, none of the specimens of asteroid and echinoid echinoderms, serolid isopods and bivalve molluscs were found to be

carrying epibiotas. Only one species of bryozoan, *Arachnopusia inchoata*, was found (infrequently) growing on sponges. In each case, the bryozoan had settled on nearby hard substratum, where it is quite abundant (Table 6.7, see also Barnes 1995a,b), and then overgrown the sponge, rather than settling directly onto the sponge.

The species compositions of the epifaunal communities of different substratum organisms were different from one another (Table 6.6). Of the pycnogonids collected from 5 metres depth, a high proportion (84%) were colonised, but only by the two species of *Celleporella*. One bryozoan species, *Fenestrulina cervicornix*, which dominates holothurians from 19 metres, was the only species found on some holothurians trawled from 50 metres, and was not found on any other substratum (biotic or abiotic) during two years of fieldwork. There were, however, some epifaunal similarities between substratum organisms. For example, the most abundant species of bryozoan colonising valves of brachiopods, *Celleporella antarctica*, also occurred frequently on *Ascolepis*, *Glyptonotus* and ascidians.

Table 6.6

Frequency of occurrence (percentage of substratum organisms bearing a given species) of some epibiotic bryozoan species on a variety of substratum organisms and depths.

Species	<i>Ascolepis</i>	<i>Glyptonotus</i>	<i>Psolus</i>			Ascidians
	(n= 114) 6 m	(n= 52) 12 m	(n= 20) 6 m	(n= 20) 19 m	(n= 18) 50 m	
<i>Celleporella antarctica</i>	35	42	6	0	0	23
<i>Beania erecta</i>	2	0	35	0	0	0
<i>Xylochotridens rangifer</i>	6	0	0	0	0	0
<i>Klugarella antarctica</i>	4	0	0	10	0	0
<i>Micropora brevissima</i>	4	0	6	3	0	1
<i>Inversiula nutrix</i>	0	16	0	0	0	0
<i>Celleporella bougainvillei</i>	19	16	2	0	0	3
<i>Fenestrulina cervicornix</i>	0	0	0	43	100	0
Other species (n)	32 (5)	26 (3)	51 (3)	44 (2)	0	73 (10)

Although colonising bryozoans covered the majority of the shells of *Liothyrella* or *Nacella* with little site specificity, a marked distribution pattern was shown on some of the

other substratum animals. Colonising bryozoans were mainly situated on the telson of *Glyptonotus*, the skeletal rod of *Ascolepis* (where living tissue had been removed, probably through predation), and on particular leg sections of pycnogonids (Figure 6.4).

The bryozoan component of these communities can be compared with the background population occurring on the surrounding physical substrata (chapter 4). When compared with rocks of similar size, the epibiota of *Liothyrella* had more species, especially in the shallower locations (Table 6.4). Underwater observations have shown brachiopod-sized stones (surface areas from $\approx 1\text{-}50\text{cm}^2$) to be moved by moderately high current and wave action conditions, which occasionally occur locally. In contrast, the motion of brachiopods observed under similar conditions is much more limited. The pedicle stalk of *Liothyrella* must afford the brachiopod a certain degree of stability by allowing it to maintain its general position despite the effects of water movement, and is probably an important influence on epibiota. The total number of species occurring on *Liothyrella* shells and on rocks of all sizes (up to roughly 50cm in length: the general physical background) was similar at all three depths.

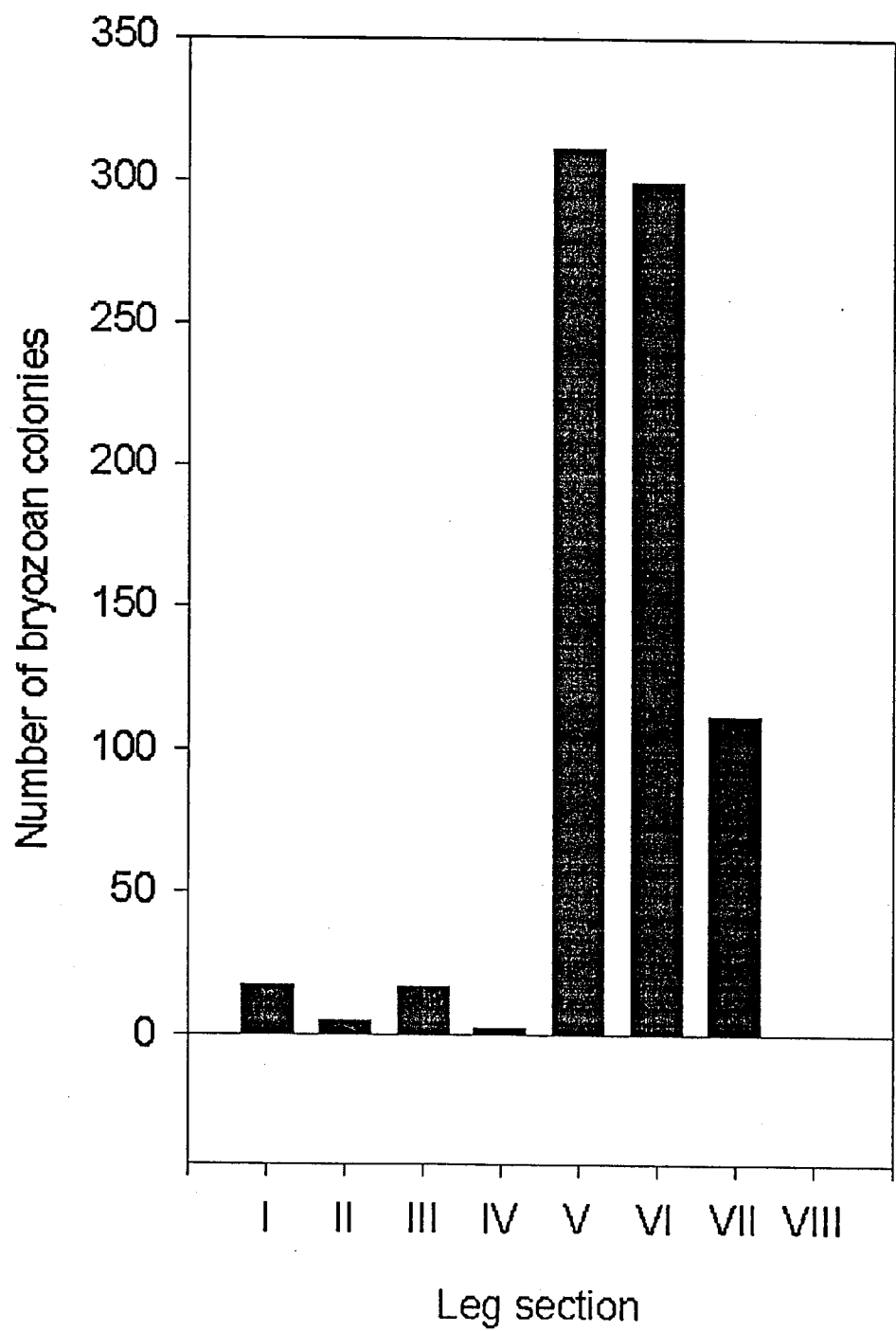
Table 6.7

Mean colony density (number of colonies per cm^2) of some bryozoan species on *Liothyrella* shells and on nearby rocks at three depths. Data for rocks from chapter 4.

Species	Colony density					
	6m		12m		19m	
	Shells	Rocks	Shells	Rocks	Shells	Rocks
<i>Celleporella antarctica</i>	1.65	0	0.44	0	1.18	0.01
<i>Beania erecta</i>	0.36	0	0.32	0	0.04	0.01
<i>Xylochotridens rangifer</i>	0.19	0	0.11	0	0.04	0
<i>Klugarella antarctica</i>	0.04	0	0.06	0	0.13	0.03
<i>Micropora brevissima</i>	0.06	0	0.06	0.05	0.22	0.90
<i>Inversiula nutrix</i>	0	0.13	0	0.29	0	1.22
<i>Celleporella bougainvillei</i>	0.02	0.18	0.01	0.10	0.03	0.16
<i>Arachnopusia inchoata</i>	0.04	0	0.03	0.02	0.10	0.0

Figure 6.4

Total number of all bryozoan colonies present on each segment of all legs summed for all pycnogonids examined (n=110). Specimens sampled from 5 metres at Factory Cove, Signy Island. All individuals were *Nymphon* sp. but could not be identified to species level.



Discussion

Cheilostome bryozoans dominated the epibiotic communities of most of the sessile benthos examined, but spirorbid polychaetes and coralline algae were also important colonisers. The proportion of these communities occupied by each taxon changed with animal species, size and habitat depth. The percentage cover of brachiopod and limpet shells by epibiota, and in particular bryozoans, (Figs 6.1 & 6.3) was very high compared to the majority of previous findings on similar substrata (see McKinney & Jackson, 1991). The reason for such high coverage may lie predominantly in the substantial life spans of polar organisms which act as a substratum, despite local larval recruitment being very low (Chapter 5).

The epibiota colonising brachiopods, limpets and holothurians were quite different, despite these host organisms being found alongside one another. Although not analysed statistically, there were no apparent tendencies for epibiota to favour particular parts of the shell on those substratum organisms which were non motile. On motile hosts, such as *Glyptonotus* or pycnogonids, surviving colonies of epibiota may largely reflect those areas incurring least abrasion during motion. The development of epibiota on *Glyptonotus* must be temporally restricted as even the adults moult (albeit occasionally). Much of the detail of this study relates to the brachiopod *Liothyrella uva* because of the particularly extensive epibiotic community development on this species.

The brachiopod *Liothyrella uva* is highly abundant in sublittoral cryptic habitats at Signy Island (Barnes, pers. obs.). Shell epibiota have been described for both fossil (Ager 1961, Taylor 1979, Kesling *et al.* 1980) and recent brachiopods (Doherty 1979, Hammond 1984, Thayer & Allmon 1991). Although the Antarctic is an area of high abundance and diversity for living brachiopods (Foster 1974, Curry *et al.* 1992), the epibiota of Antarctic brachiopods have remained undescribed. The overgrowth and smothering of young brachiopods by bryozoans, observed in this study, has also been reported from populations of brachiopods in New Zealand (Doherty 1979), which biogeographically probably represents the closest study to the present.

The number of epibiotic species found on brachiopod shells was found to be higher than rocks of a similar size but approximately equal to that on larger rocks (Table 6.5). The number of species present may reflect substratum stability: the smaller the rock, the lower the energy required to move it and thus the greater the frequency of movement and disturbance or damage to encrusting benthos. The effect of depth, in terms of stability (with respect to the effect of waves and current), is proportionally greater on smaller rocks (chapter 4). A number of other factors, such as depth-related variations in larval dispersal of the bryozoan species and physical effects like ice scour will also generally influence the number and abundance of species with depth. In this study, only a small increase with depth was found in the number of species present on both physical hard substrata and *Liothyrella* shells. In contrast there was a seven-fold increase with depth in the number of bryozoan species found on small rocks. Depth-related larval dispersal variations and ice scour should presumably affect shells and rocks at the same depth location equally, thus substratum stability probably explains the great increase in the number of bryozoan species on the smaller rocks with depth.

The clumping habit of *Liothyrella* seems to have little effect on epifaunal communities, although this effect needs closer examination by examining a greater number of specimens of a wider range of sizes and clump sizes. It is possible that clumping will affect the stability of *Liothyrella* communities, through its impact on drag in high currents, similar to the effect described for algae on mussels (Witman & Suchanek 1984). For most communities of *Liothyrella*, at Signy Island, this effect is likely to be small because the brachiopods live largely in cracks and crevice locations, where water movement is reduced.

The community composition and density (colonies/cm²) of the bryozoan species found in a previous study of physical substrata from similar localities (chapter 4) were significantly different from those of the organism substrata in this study at each depth (Tables 6.5 & 6.7, chi square tests, all $P < 0.001$). For example some species, such as *Inversiula nutrix* Jullien, which is the most abundant background species on nearby rocks, were virtually unrepresented in the epibiotic communities of animals. Conversely *Fenestrulina cervicornix* was only ever found epibiotically on holothurians, whereas

Micropora brevissima occurred in relatively similar proportions on organism and non-organism substrata. Some bryozoan species occurred, or were dominant, on a number of communities of epibiota on different animals (Table 6.8), whilst others only occurred on one type of animal. The bryozoan fraction of an epibiota may therefore be divided into four broad types of species: generalists common on all substrata (such as *Celleporella bougainvillei*), host-specific epibiotic species (such as *Fenestrulina cervicornix*), host-low specificity epibiotic species that commonly settled on organisms though were rare on rocks (such as *Celleporella antarctica*), and species that occurred commonly on the rocks or 'background' of the location (such as *Inversiula nutrix*). These are shown in Table 6.8. Species of generalist, host-specific and host-nonspecific nature were all dominant on at least one of the organism hosts (Table 6.9). On *Liothyrella*, the abundance or dominance of these species categories remained largely unchanged at different depths, although the abundance of the host-specific species *Fenestrulina cervicornix* on holothurians changed from 0% of colonies present at 6 m depth through 43% at 18 metres to 100% at 50 metres.

Table 6.8

A classification of some common Antarctic cheilostome bryozoans based on their occurrence as epifauna on biotic and abiotic substrata.

Bryozoan species type	Example species
Generalists Species which occur widely on rocks, stable hard substrata and most animal hosts.	<i>Celleporella bougainvillei</i> <i>Ellisina antarctica</i> <i>Arachnopusia inchoata</i>
Host-specific species Species found only on specific animal hosts.	<i>Fenestrulina cervicornix</i>
Low specificity epibiotic species Species which occur widely on organisms, but rarely on rocks.	<i>Celleporella antarctica</i> <i>Xylohotridens rangifer</i>
Background species Species which occur widely on rocks, but rarely on organisms.	<i>Inversiula nutrix</i> <i>Escharoides tridens</i> <i>Smittina rogickae</i>

Table 6.9

Abundance of epibiotic bryozoan species on various substrata. For each substratum organism, rank 1 is the most frequent bryozoan epibiotic species, rank 2 the second most abundant, and so on.

Substratum organism	Bryozoan abundance rank			
	1	2	3	4
<i>Liothyrella</i>	Ca	M	Ar	K
<i>Nacella</i>	Cb	Ca	L	I
<i>Ascolepis</i>	Ca	Cb	X	Ha
<i>Glyptonotus</i>	Ca	Cb	I	Ar
ascidians	L	Ca	Ar	H
<i>Psolus</i>	Fc	L	Ai	K

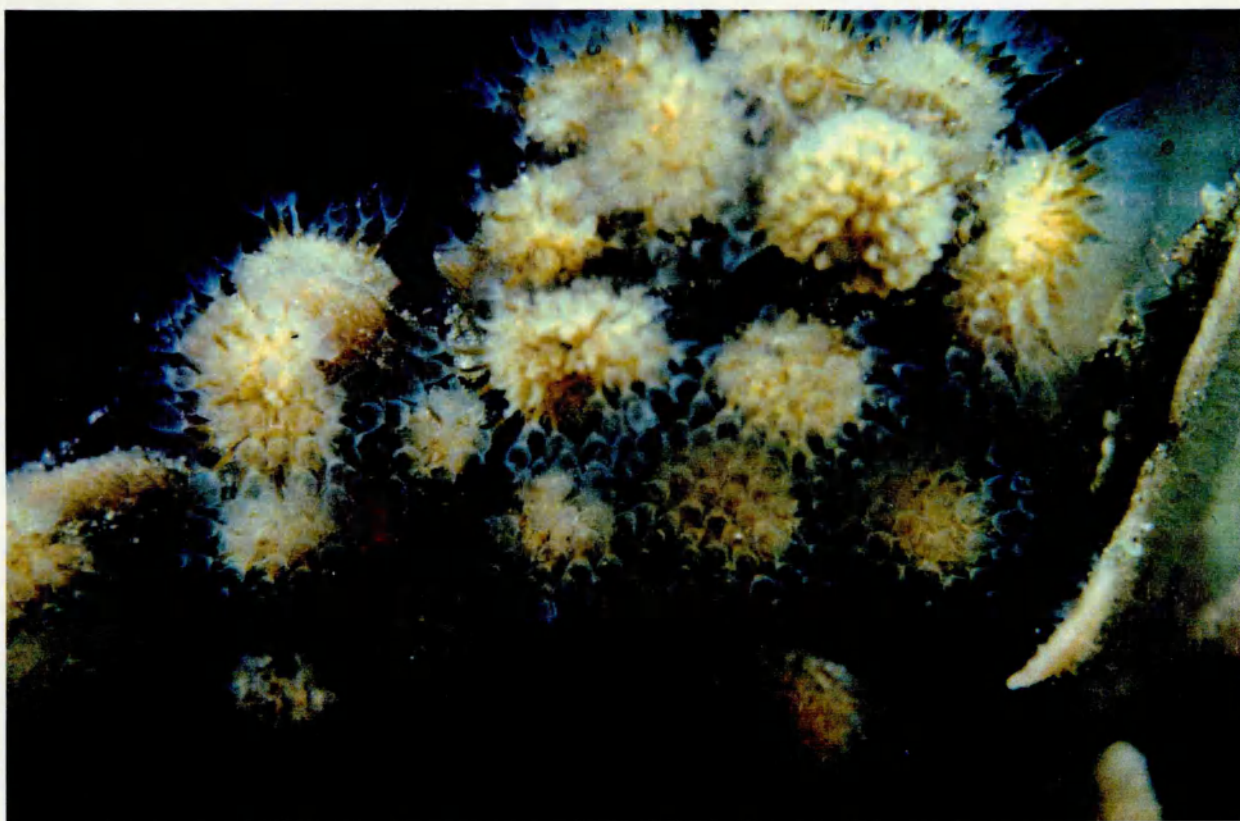
The species abbreviations are : Ca *Celleporella antarctica*, Cb *Celleporella bougainvillei*, L *Ellisina antarctica*, Fc *Fenestrulina cervicornix*, M *Micropora brevissima*, Ar *Arachnopusia inchoata*, X *Xylochotridens rangifer*, I *Inversiula nutrix*, Ai *Aimulosa antarctica*, K *Klugarella antarctica*, Ha *Harpecia spinosissima*, H *Hippadanella inerma*.

One interesting area of further research, not covered in this study, would be to examine the distribution of epibiota on shells with respect to the degree of patchiness in settlement and recruitment in relation to the density of colonisers. Such a study could also investigate whether the density of a given epibiotic taxon was similar in circumstances where it did or did not predominate in the community.

The communities of epibiota on sublittoral organism substrata at Signy Island are quite varied in composition. Bryozoans dominate many of these assemblages, but are overgrown by both sponges and under certain conditions the coralline alga *Lithothamnion*. The bryozoan component of epibiotic communities may be complex and may involve as many or more species than occurring on abiotic hard substratum, as well as different species.

Plate 3

A branch of the erect bryozoan *Alloeflustra tenuis* covered by colonies of the bryozoan *Beania erecta*.



Colonisation of bryozoans: two erect species of bryozoans

Introduction

One of the most challenging difficulties facing sessile marine organisms is competition for space, as this is frequently a limiting resource (Connell 1961b, Dayton 1971, Paine 1974, Jackson 1977). Associated with this is the danger of overgrowth, usually resulting in the death of the overgrown species (Jackson 1977, Rubin 1985, Lopez Gappa 1989). In many sublittoral epibenthic environments colonial organisms have been shown to be dominant over solitary organisms (Jackson 1977, Keough 1984). Bryozoans are generally poor competitors compared with other colonial phyla, such as sponges or ascidians (Kay & Keough 1981, Jackson & Winston 1982, Russ 1982, Keough 1984) and as a result they tend to be abundant in ephemeral habitats (McKinney & Jackson 1991, chapters 4 & 6).

A number of studies of interactions between different taxa of epibiota, and bryozoans in particular, have been made in temperate and tropical latitudes. These have mostly concerned bryozoans as the colonising (Stebbing 1972, Doherty 1979, Russ 1982, Jackson & Winston 1982, Whitman & Suchanek 1984) rather than the colonised taxa (Stebbing 1971). To date however no such studies have been undertaken in polar areas, where bryozoans have been established to be an important component of benthic sessile communities (Bullivant 1961, 1967, Winston & Heimberg 1988, Galéron *et al.* 1992).

Various aspects of Antarctic bryozoan distribution have been considered in this section, culminating with the investigation of bryozoans as colonising or fouling agents on other organisms, in the previous chapter. This chapter examines the colonisation or fouling of bryozoans. The extent of colonisation together with the distribution and taxonomic composition of the epibiota was investigated for two erect cheilostome species, *Alloeflustra tenuis* and *Nematoflustra flagellata*. Morphological differences between the two host species were examined with respect to possible influences on the characteristics of their respective epibiota. Although the main study focused on specimens collected from 40 m, additional specimens of these species were also collected from 150 m for comparison.

Materials and methods

Study site and species

The study site was at Outer Island in Borge Bay. The site is characterised by low current regimes and by rock rubble substrata overlain by a thin layer of sediment. Small rock faces (0.5-1.5 m high) occasionally protrude from the otherwise shallow sloping area. The annual variation in temperature ranges from approximately -1.9°C in winter to $+0.5^{\circ}\text{C}$ in summer and, together with local primary productivity and sea-ice duration, is described for this locality by Clarke *et al.* (1988).

Erect planar species were chosen for the study as these are easy to detach from the substratum and collect, and also facilitate detailed examination of epibiota by microscopy and photography. Two erect planar species are common in the sublittoral (40 m) at Signy Island: *Alloeflustra tenuis* and *Nematoflustra flagellata*, as described in chapter 3. Like the similar temperate species *Flustra foliacea* (Stebbing 1971, De Kluijver 1993), these two species are locally very abundant on the shallow sloping rock surfaces that often protrude from the sediment. The study species both grow on the shallow slopes and the small vertical outcrops. The two species of cheilostomes studied are both unilaminar; that is they are composed of one sheet of zooids. The lophophores protrude only on one side, the same side as the avicularia occur, here termed the front surface. The front surface faces downwards towards the substratum in *A. tenuis*, but upwards towards the water column in *N. flagellata*.

Sampling

Between 1991 and 1992, 148 specimens of *Alloeflustra tenuis* and 158 specimens of *Nematoflustra flagellata* were collected, using SCUBA. In addition five Agassiz trawls at 150 m, each of 20 minutes duration, in Normanna Strait between Signy Island and nearby Coronation Island, provided 9 specimens of *A. tenuis* and 16 specimens of *N. flagellata* from deeper water for comparison.

Each colony of *Alloeflustra tenuis* and *Nematoflustra flagellata* was examined carefully with a stereomicroscope and every individual or colony of epibiota was identified to the lowest feasible taxonomic level (species in the case of Bryozoa, family for Annelida and just 'sponges' and 'ascidians' etc. for others), and counted. Each host specimen was then measured. In this study simple total length (measured from the colony base to growing tip) proved most satisfactory; other measures including width or branch number and various combinations thereof, were tried but proved less useful. Photographs were taken of the front and rear surfaces of each specimen, and the subsequent transparencies were projected onto a regular grid of 7700 points. The area of each epibiotic colony or individual was estimated from the array of points it covered (similar to the methods used for measuring epibiota on rock faces in chapters 2 & 3). These measures were then summed for each taxonomic group. Overall flustrid colony area was also estimated in this manner, which allowed overgrowth of each taxonomic group to be expressed as total percentage area of the host occupied as well as the number of occurrences.

A few observations were made on the epibiota of other locally occurring erect bryozoans. Observations were also made on the functioning of avicularia and vibracula, both *in situ* and in laboratory aquaria, as their purpose is still uncertain (Winston 1984, 1986). Twenty specimens of each of the two study species were held in through-flow aquaria maintained at a similar temperature to field conditions. The orientation of half of these specimens was reversed and observations made on avicularia behaviour and sedimentation of colony surfaces.

Results

Taxa present as epifauna

Bryozoans, mostly Cheilostomata, were responsible for over 80% of colonisation (by area), on both surfaces of both species. Although 20 species of cheilostome bryozoans were recorded (16 encrusting, 4 erect), one encrusting species, *Celleporella antarctica*, was

responsible for most of the total area colonised. Spirorbid polychaetes occupied much of the remaining area, but other tubicolous polychaetes and tanaid crustaceans, cnidarians and entoprocts also occurred, whilst brachiopods and sponges were uncommon (Table 7.1).

Table 7.1

Epifauna occurrence and abundance on front and rear surfaces of the bryozoans *Alloeflustra tenuis* and *Nematoflustra flagellata*. The frequency of occurrence of each taxon is indicated by percent values. Values over 10% are highlighted in bold.

Taxa		<i>Alloeflustra</i>		<i>Nematoflustra</i>	
		Front	Rear	Front	Rear
Porifera	sponges	1.6	0	0	1
Cnidaria	hydroids	3.3	31.7	1.6	25.2
	octocorals	0	1	0	1.6
	anemones	0	1	0	1.6
Annelida	spirorbrids	25.5	72.7	20.9	85.5
	tubicolous polychaetes	8.2	50	1	6.4
Crustacea	tubicolous tanaids	2.4	10.6	1.6	8.9
Entoprocta	<i>Barentsia</i> sp.	1	4.1	0	4.9
Brachiopoda	lamp shells	1	0	1	1
Bryozoa	<i>Aimulosa antarctica</i>	1	0	1	1.6
	<i>Amphiblestrum familiaris</i>	1	0	3	12
	<i>Alloeflustra tenuis</i>	1	1.6	3.3	9.8
	<i>Arachnopusia inchoata</i>	14.5	31.7	14.5	31.7
	<i>Beania erecta</i>	62	8	1	1
	<i>Camptoplites bicornis</i>	1	3.3	0	1
	<i>Celleporella antarctica</i>	14.5	100	89.4	97.6
	<i>Celleporella bougainvillei</i>	3	4	1	6
	<i>Celleporella dictyota</i>	0	1	0	1
	<i>Escharoides tridens</i>	0	2.4	0	1
	<i>Ellisina antarctica</i>	38	39.1	12	28
	<i>Fenestrulina rugula</i>	0	1	0	2.4
	<i>Harpecia spinosissima</i>	0	3	15	12
	<i>Himantozoum antarcticum</i>	0	4.9	0	10.6
	<i>Inversiula nutrix</i>	3	4.9	1	6
	<i>Klugerella antarctica</i>	3.3	3.3	1.6	2.4
	<i>Lacerna eatoni</i>	48	1	0	1
	<i>Micropora brevissima</i>	7	9	1	10.6
	<i>Nematoflustra flagellata</i>	0	1	0	1
	<i>Valdemunitella lata</i>	0	0	1	1
	cyclostomatans	64.5	75.5	46.4	75.5
Chordata	ascidians	25.5	39.1	5.5	29.1

Table 7.1 shows a high degree of similarity between the epibiota of the two bryozoan hosts in terms of overall taxonomic composition. However, there were distinct differences in the extent of colonisation between front and rear surfaces, and in the proportions of bryozoan species.

Differences between front and rear surfaces

In both *Alloeflustra tenuis* and *Nematoflustra flagellata* there were significant differences in the extent to which the front and rear surfaces were colonised (Table 7.2; Mann-Whitney U-test, $P < 0.01$ for both species). The front surface of both species was colonised to a much lesser extent than the rear, and in addition the front surface of *N. flagellata* was colonised to a lesser extent than that of *A. tenuis*. The mean number of bryozoan species occurring on the front surface of *A. tenuis* was significantly higher than that of *N. flagellata*, though numbers were similar on the rear surface.

Table 7.2

Extent of colonisation on front and rear surfaces of *Alloeflustra* (A) and *Nematoflustra* (N). Figures are expressed as sample medians with range in brackets. Each species was sampled from two depths as shown.

Variable	40 M (Depth)		150 M (Depth)	
	A	N	A	N
% Area of front surface colonised	3.2 (0-54)	1.1 (0-10)	0.5 (0-2.0)	0.0 (0-1.0)
% Area of rear surface colonised	75 (0-99)	67 (0-99)	10 (2-25)	3 (1-20)
No. species on front surface	3.0 (0-6)	2.0 (0-4)	1.0 (0-1)	0.0 (0-1)
No. species on rear surface	3.0 (0-7)	2.0 (0-9)	2.0 (0-4)	1.0 (0-4)
Bryozoa as % of epibiota on front	95 (0-100)	100 (0-100)	100 (0-100)	100 (0-100)
Bryozoa as % of epibiota on rear	90 (13-100)	93 (0-99)	30.0 (0-70)	27.5 (0-80)
Sample size	123	123	9	16

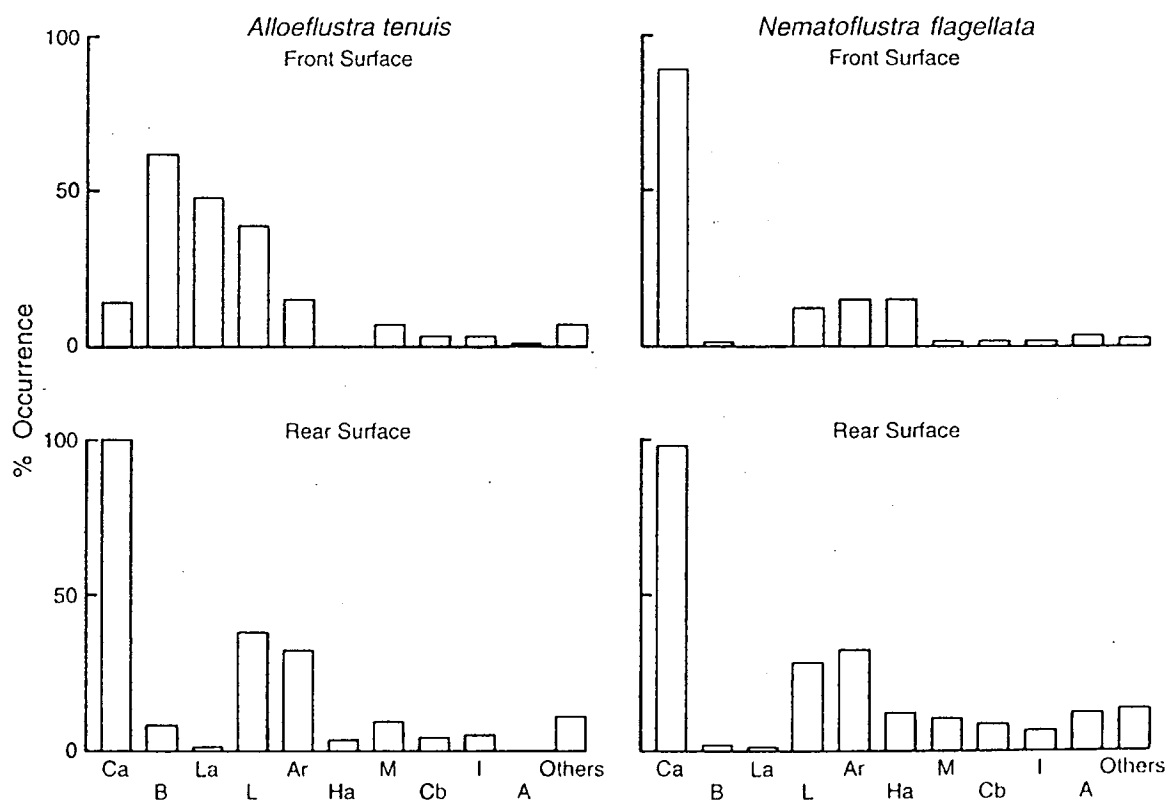
The species composition of the colonising community on each surface, and on each species, was found to be different (Fig. 7.1). The difference was most noticeable with *A. tenuis*: the two most abundant colonising species on the front surface, *Beania erecta* and *Lacerna eatoni* (Busk), occurred on less than 10% of the rear surfaces. Most of the other

species had higher frequencies of occurrence on the rear surface, and in the case of *Celleporella antarctica*, dramatically so.

The four most abundant species on *Nematoflustra flagellata* occurred in similar proportion on each surface, although the frequency of occurrence on the rear was mostly slightly higher. The main difference in epibiotic species composition between the surfaces, was the prevalence of the rarer colonising species, which were generally present only on the rear surface. In summary the epibiotic species composition, as well as species number and percentage area covered by epibiota, was similar between the rear surfaces of *A. tenuis* and *N. flagellata*, but different between the front surfaces.

Figure 7.1

Percentage occurrence of encrusting cheilostome bryozoans on front and rear surfaces of *Alloeflustra tenuis* and *Nematoflustra flagellata*. The species are Ca, *Celleporella antarctica*; B, *Beania erecta*; La, *Lacerna eatoni*; L, *Ellisina antarctica*; Ar, *Arachnopusia inchoata*; Ha, *Harpecia spinosissima*; M, *Micropora brevissima*; Cb, *Celleporella bougainvillei*; I, *Inversiula nutrix*; A, *Amphiblestrum familiaris*



Effect of host size on colonisation by epifauna

The degree of epifaunal colonisation was significantly related to the size of the two flustrids in a number of respects (Table 7.3). Total percentage area covered by epifauna increased with host size, although only on the rear surfaces and the variance was very high. The number of phyla occurring increased with height on the front surface of *Alloeflustra tenuis* and the rear surface of *Nematoflustra flagellata*, and the number of bryozoan species increased with size on both surfaces of both host species. The total number of bryozoan colonies increased similarly, although to some extent this might be expected if the number of colonist bryozoan species increased with host size (Table 7.3).

Table 7.3

Relationships between size of host bryozoan and level of colonisation by epifauna that showed statistical significance. All other possible combinations showed non significant results ($P>0.05$). Analysis of variance (ANOVA) of relationship between length of host colony and variable: F = variance ratio, P = probability of result arising through chance.

Variable	<i>Alloeflustra</i>			<i>Nematoflustra</i>		
	Surface	F	P	Surface	F	P
% Area covered	rear	9.3	0.003	rear	6.2	0.015
No. Phyla present	front	8.0	0.006			
				rear	13.3	<0.001
No. Bryozoan species present	front	65.3	<0.001	front	35.5	<0.001
	rear	99.9	<0.001	rear	29.0	<0.001
No. Bryozoan colonies present	front	20.2	<0.001	front	58.6	<0.001

Interactions between epifauna

A number of associations seemed to be present between the colonising cheilostome species. Those species pairs which showed statistically significant ($P<0.01$) correlations in occurrence or abundance are shown in Table 7.4. Associations that involved species with low frequencies of occurrence must be viewed with caution, as the correlations will have been calculated from a small number of data points (Fig. 7.1). On the front surface of *Alloeflustra tenuis*, the occurrence (but less so abundance) of *Beania erecta* and *Lacerna eatoni* were significantly linked, as were *Ellisina antarctica* and *Celleporella antarctica*.

Table 7.4

Pairs of colonising cheilostome bryozoan species which show statistically significant ($P < 0.01$) relationships in occurrence or abundance. Occurrence (Occur) was defined as the fraction of colonies examined which had this species, and abundance (Abund) was defined as the number of separate instances of the species on each colony examined. Those species pairs that occurred on >10% of colonies are indicated with a ✓. The table gives Pearson product-moment coefficients. All the other possible 254 species pairings, showed non significant interactions/relationships.

Surface	ALLOEFLUSTRA			NEMATOFLUSTRA		
	Epifauna sp.	Occur	Abund	Epifauna sp.	Occur	Abund
Front	✓ <i>C.antarctica</i> * <i>B.erecta</i>	-0.352		✓ <i>C.antarctica</i> * <i>H. spinosissima</i>		0.286
	✓ <i>C.antarctica</i> * <i>L.eatoni</i>	-0.302		✓ <i>C.antarctica</i> * <i>A.inchoata</i>		0.217
	✓ <i>C.antarctica</i> * <i>E.antarctica</i>	0.260	0.332	<i>C.antarctica</i> * <i>C.bougainvillei</i>	-0.314	
	✓ <i>B.erecta</i> * <i>L.eatoni</i>	0.417				
	✓ <i>L.eatoni</i> * <i>A.inchoata</i>		0.298			
	<i>C.antarctica</i> * <i>M. brevissima</i>	0.222				
	<i>C.antarctica</i> * <i>C.bougainvillei</i>	0.275	0.345			
	<i>C.antarctica</i> * <i>I.nutrix</i>	0.310				
	<i>B.erecta</i> * <i>C.bougainvillei</i>	-0.214				
	<i>E.antarctica</i> * <i>M.brevissima</i>		0.308			
	<i>E.antarctica</i> * <i>C.bougainvillei</i>		0.436			
	<i>M.brevissima</i> * <i>C.bougainvillei</i>	0.211				
	<i>M.brevissima</i> * <i>I.nutrix</i>	0.235	0.310			
Rear	✓ <i>E.antarctica</i> * <i>A.inchoata</i>	0.296	0.230	✓ <i>E.antarctica</i> * <i>A.inchoata</i>	0.250	
	<i>E.antarctica</i> * <i>H.spinosissima</i>		0.293	✓ <i>A.inchoata</i> * <i>M.brevissima</i>		0.256
	<i>E.antarctica</i> * <i>M.brevissima</i>		0.304	✓ <i>H.spinosissima</i> * <i>M.brevissima</i>	0.282	0.231
	<i>H.spinosissima</i> * <i>I.nutrix</i>		0.255	<i>B.erecta</i> * <i>L.eatoni</i>	0.272	0.239
	<i>M.brevissima</i> * <i>I.nutrix</i>	0.381	0.288	<i>L.eatoni</i> * <i>A.inchoata</i>		0.398
				<i>M.brevissima</i> * <i>C.bougainvillei</i>		0.216

The species *B. erecta* and *L. eatoni* were, however, negatively associated with *C. antarctica*. The five most abundant colonising species on the front surface of *A. tenuis* occurred mostly in three distinct groupings: the two species pairs described above and the single species *Arachnopusia inchoata* (which showed no significant associations with other species).

The associations of these same species on the rear surface were very different, and in general, there were fewer correlated species. Notable linked occurrences and

abundances were those between *Ellisina antarctica* and *Arachnopusia inchoata* and between *Micropora brevissima* Waters and *Inversiula nutrix* Jullien. On the front surface of *Nematoflustra flagellata* there were comparatively few species associations: *Arachnopusia inchoata* and *Harpecia spinosissima* (Calvet) were both positively correlated with *Celleporella antarctica* with respect to abundance, though not occurrence. On the rear surface of *N. flagellata* (as on that of *A. tenuis*) the occurrence of *E. antarctica* and *A. inchoata* were positively correlated. *H. spinosissima* and *M. brevissima* were the only species pair positively linked with respect to both occurrence and abundance on the rear surface of *N. flagellata*.

By far the highest correlation values, however, linked the occurrence of species on the front surface and rear surfaces of the same colony. With the exception of *Lacerna eatoni*, in the seven commonest species of colonising cheilostomes occurring on *Alloeflustra tenuis* it was found that if a species occurred on the front surface it was highly likely to be found also on the rear. In contrast on *Nematoflustra flagellata*, this was the case for less than half of the common species that occurred.

Sedimentation and avicularian behaviour

The upward facing surface (normally the rear surface of the colony as defined by zooid orientation) of *Alloeflustra tenuis* collected considerable detritus both in the field and in aquaria. This sedimentation occurred regardless of whether the colony front surface or the colony rear surface faced upwards and no avicularian behaviour was noted in connection with the fallout of detritus. Avicularian behaviour prevented sedimentation on the upwards facing front surface of *Nematoflustra flagellata* but when the rear surface faced upwards (which occurs rarely in the field) it became loaded with sediment. A beating response of *N. flagellata* avicularia was triggered, on nearly all observed occasions, by disturbance from settling material or errant epibiota (such as amphipods) crawling on the surface. Such a response consisted of each vibraculum beating out of phase to create a wave towards the colony base, occasionally involving vibracula throughout the entire colony.

Differences in colony morphology and epifauna with depth

Though similar at the zooidal level, the colony morphology of *Alloeflustra tenuis* and *Nematoflustra flagellata* collected from 150 m was clearly different from those at 40 m. The deeper specimens grew much taller, with thinner branches (fewer zooids in width), and the strong curling of branches evident in *N. flagellata* at 40 m did not occur at 150 m. The area of epibiotic colonisation was significantly less on both surfaces of both species (ANOVA, $p < 0.01$), than on the shallower occurring specimens, by a factor of 6 or more (Table 7.3). Despite the overall lower rate of colonisation in deeper water specimens, the ratio of the degree of colonisation of upper and lower surfaces in the same colony, remained similar to that at 40 m. The mean number of encrusting bryozoan species was also much lower in the deeper specimens, particularly on the front surface. *Celleporella antarctica* was the most abundant colonising species at 150 m, as was also the case at 40 m.

Discussion

The erect bryozoans *Alloeflustra tenuis* and *Nematoflustra flagellata* have similar morphology and occur in similar habitats. There are, however, differences in colony orientation, growth rate (*N. flagellata* may grow three times faster: see chapter 10) and the ratio of avicularia to autozooids. Colony orientation (whether the front surface points up or not) may be strongly linked to the ratio and function of avicularia in these two species. The avicularia of *N. flagellata* occurred at the anterior of every autozoooid and were greatly elongated; these elongated structures are generally termed vibracula. In *A. tenuis* the avicularia are smaller and much scarcer. Stereomicroscope observation of living *N. flagellata* showed that when diatom chains or detritus landed on the front surface, they were quickly removed by synchronous beating of the vibraculae, as observed by Winston (1991). The principal function of the vibracula in *N. flagellata* would therefore appear to be cleaning, as has been observed for *Discoporella umbellata* (Cook 1963).

Coordinated avicularian behaviour was not noted by *Alloeflustra tenuis* and unlike *Nematoflustra flagellata* the front surface accumulated considerable sedimentation if facing upwards. Thus avicularia of *A. tenuis* do not perform an obvious cleaning function. As with the avicularia of many species, the functions of the avicularia of *A. tenuis* remain unknown (Winston 1984, 1991), although a limited defense function seems most plausible.

The likely differences in growth rate (chapter 10) might explain the different degrees of area colonisation on the front surface, but not the differences in epizoite species composition or the similarity in epizoite species composition and area of rear surfaces colonised. The zooids of *Alloeflustra tenuis* and *Nematoflustra flagellata* face opposite directions (one towards the sediment and the other towards the water column), so orientation would also fail to explain the similarities in pattern of colonisation of rear surfaces. The abundance and morphology of the avicularia of *N. flagellata*, however, may help explain many of these differences. Suspension feeding epibiota, such as bryozoans, need to avoid accumulation of detritus which might inhibit feeding activity. This can be achieved by either colonising vertical or overhanging substrata, where settlement of detritus or epibiota will be low, or by having an active method of discouraging settlement. If avicularia were effective, then most colonising species would occur more frequently on rear surfaces, whereas those few colonising species capable of settlement and overgrowing avicularia, might have greatest frequency on the front surfaces.

The composition of colonising species of the surfaces of the two species (Fig. 7.1 and Table 7.1) shows that the abundance of most species is greater on the rear than the front. The fact that three species occurred in abundance on the front surface of *Alloeflustra tenuis*, compared with only one species on *Nematoflustra flagellata* was possibly a consequence of the greater density and the cleaning function of *N. flagellata* avicularia. The three species that occurred in abundance on *A. tenuis* often settled directly on the front surface and overgrew avicularia. *Celleporella antarctica*, the one abundant species on the front surface of *N. flagellata*, usually grew over to the front surface from the rear, thus avoiding direct settlement on the protected surface. When growing over the front surface, the colonies of *C. antarctica* often grew around each avicularia. These avicularia,

however, continued to function even when surrounded by the colony of *C. antarctica*, so protecting the overgrowing colony of *C. antarctica* from detritus fallout or being colonised itself.

The study of fouling communities on molluscan and brachiopod shells at Signy Island (chapter 6, Barnes & Clarke 1995b) suggested that most bryozoan colonisers could be classified into one of four broad groups: generalists, host-specific epibiotic species, low specificity epibiotic species or species locally abundant on most substrata. Most of the fouling bryozoan species found in this study could be ascribed to the latter two groupings. Two of the species which were found to occur most frequently on a variety of organismal substrata (low specificity epibiotic species), *Celleporella antarctica* and *Ellisina antarctica*, were also two of the most abundant on *Alloeflustra tenuis* and *Nematoflustra flagellata*. A number of species occurring commonly on local hard-substrata colonised the two bryozoan hosts studied here in lower proportions, and were particularly rare on the front surface of *N. flagellata*. The structure, abundance and behaviour of vibracula may work particularly well at preventing settlement or growth of these particular species, compared with the smaller and occasional avicularia of *A. tenuis*.

Other comparable erect species of cheilostome bryozoans are uncommon in the locality studied, although observations of a few specimens of *Carbasea ovoidea* Busk, a species without avicularia, revealed intense colonisation on both surfaces. Of the 20 colonies of the rigid erect species *Cellarinella watersi* observed, only one showed any colonisation. In this locality both these species were thought to be much shorter lived than *Alloeflustra tenuis* and *Nematoflustra flagellata* (chapter 10).

The epibiota had no detectable influence on the growth rate of the host colony (chapter 10), though this may be because the result was based on a small sample. In the similar temperate species *Flustra foliacea* (Stebbing 1971), A significant difference in growth was noted, between specimens with and without epibiota.

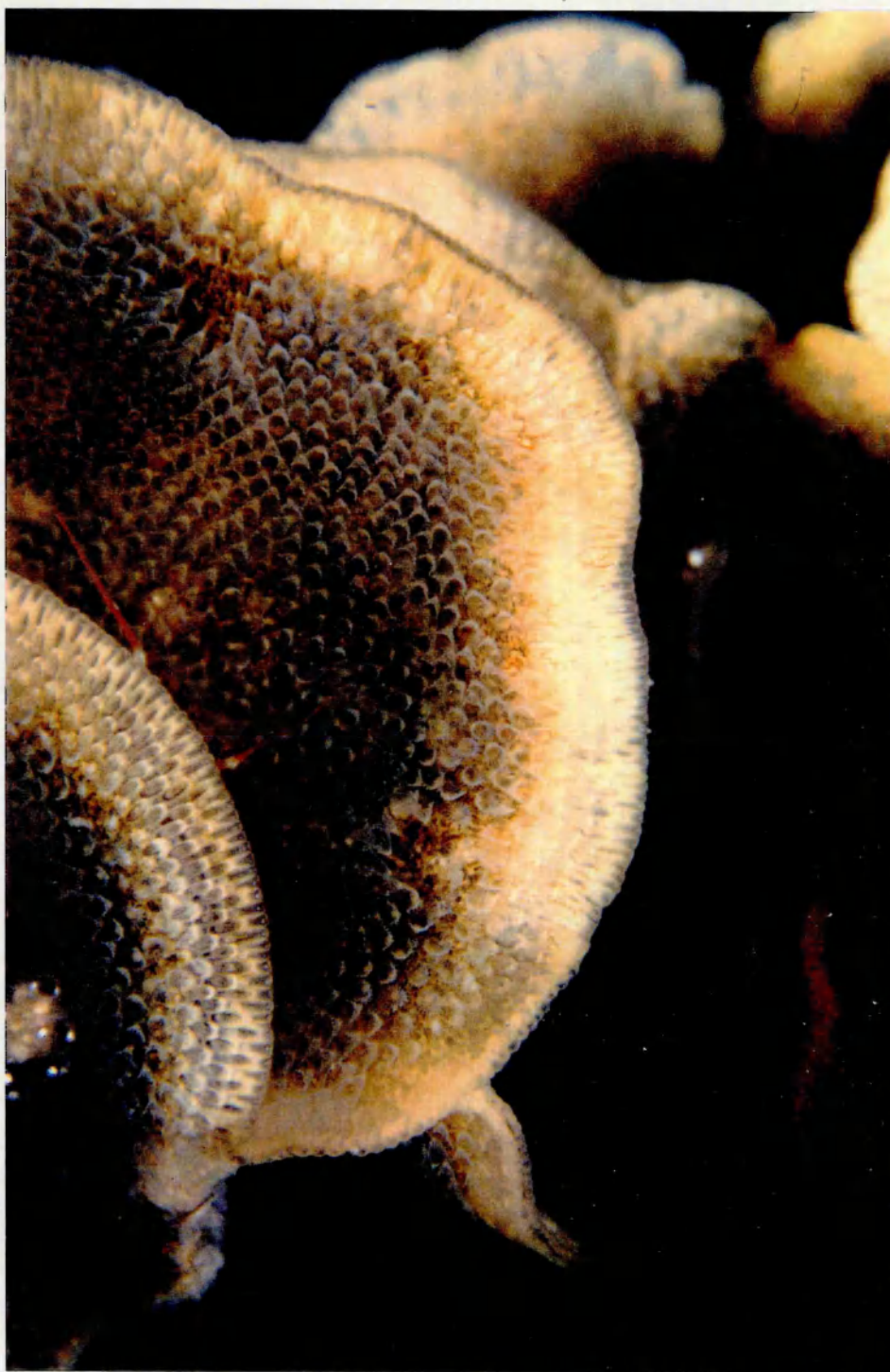
Concluding remarks

This chapter concludes a wide range of studies investigating the distributional ecology of bryozoans with respect to other shallow water Antarctic benthos. In the intertidal at Signy Island bryozoans are one of the few taxa to be present, albeit rare and in the sublittoral they are abundant and play an important role in community development. Encrusting bryozoans are found dominating ephemeral and newly exposed substrata of both abiotic and biotic nature. They are, however, overgrown and outcompeted eventually by most other encrusting taxa, typically sponges and ascidians. The diversity and abundance of bryozoans on rock faces is thus associated with the high disturbance frequencies experienced in the shallow marine environment at this location. In the soft substrata and deeper circalittoral water at Signy Island, erect bryozoans become more numerous (and in places the most abundant taxon) where they act as secondary substrata for encrusting bryozoans. To understand more about the ecology of this abundant taxon, the lifestyles and systematics must be examined. One of the most marked characteristics of the Southern Ocean is the intensity and brevity of primary production, thus the most obvious point to begin a study of lifestyles is to investigate feeding periodicity, activity cues and food availability.

Section 3. Life histories

Plate 4

The bryozoan *Arachnopusia inchoata* with lophophores everted.



Feeding activity: seasonal variations in four species of bryozoan

Introduction

Section two provided an outline to patterns, dynamics and influences on sublittoral benthic communities at Signy Island, whilst illustrating how little is generally known of such organisms in the Antarctic as a whole. The functioning of such communities, however, has also been little studied and their feeding biology is virtually unknown. Before this chapter, only one study has been undertaken of feeding physiology in Antarctic suspension feeders. This was a laboratory study of feeding rate in the bryozoan *Himantozoum antarcticum* (Sanderson *et al.* 1994). This chapter describes the first *in situ* study of feeding in Antarctic benthos.

The coastal marine environment of Antarctica is characterised by a brief, but intense, summer period of open-water phytoplankton productivity alternating with a period of winter sea ice; the latter is associated with low light, reduced food availability for suspension feeders, and minimal disturbance by water movement (Clarke 1988). For benthic suspension feeders, the winter period has long been considered one of starvation and Gruzov (1977) reported benthos from the Davis Sea as entering a state of 'hibernation' in winter. The established view is thus one where the low levels of water column chlorophyll in winter imposes a seasonal resource limitation on polar suspension feeders (Clarke 1988). Where metabolic costs are high (for example in herbivorous zooplankton such as copepods) energy is provided in winter from large lipid stores; where metabolic costs are low (for example in sessile suspension feeders) winter energy costs can be met from normal tissue lipid and protein levels (Clarke & Peck 1991).

The feeding apparatus, mechanism of particle capture, feeding behaviour and nature of prey has been the focus of many temperate studies of suspension feeding taxa, and bryozoans in particular. Such studies have been principally carried out by examining the behaviour of laboratory specimens under microscope and through theoretical reasoning. Despite much controversy between Bullivant (1968), Strathman (1971, 1982) and Best &

Thorpe (1983) the general and current conclusion is that a number of methods are used to capture particles, including occasional reversing of the cilia (which beat to cause the feeding current), flicking of entire tentacles and eddying effects (Best 1985, Hunter & Hughes 1993). Such methods and flow rates of generated feeding currents have been found to alter with environmental conditions, particularly with food concentration (Best & Thorpe 1983, 1986, 1993, Fisher 1989) and local flow rate (Okamura 1987, 1990).

Considering the intense seasonality of the Antarctic marine environment, one of the most pressing questions concerning the biology of suspension feeders is the length of the period during which feeding could take place. This study aimed to investigate the seasonal pattern of feeding activity in four Antarctic bryozoans, and in particular the duration of the period of winter starvation. The study also intended to determine how the timing of the summer feeding period might relate to the seasonal variation in food availability, temperature and ice cover.

Materials and methods

Study sites and species

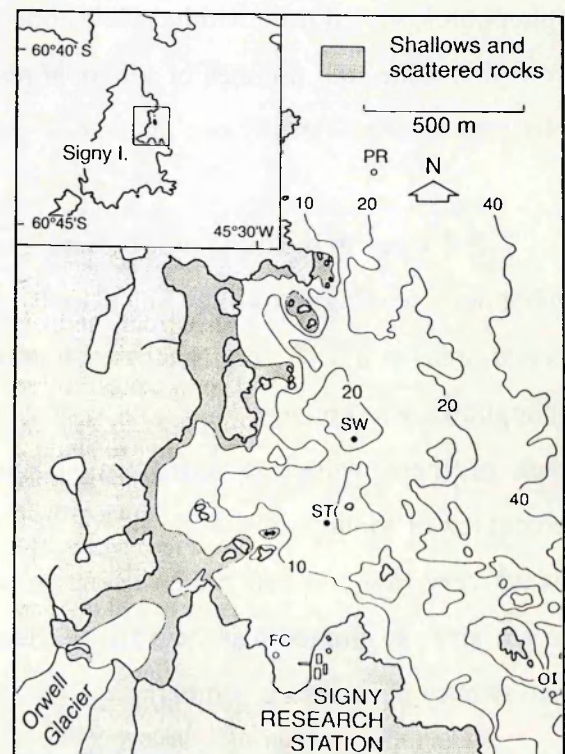
This study was undertaken in Factory Cove, Powell Rock and Outer Island in Borge Bay. The locations of the study sites and the oceanographic stations are shown in Fig. 8.1. At this latitude, daylength varies from a summer maximum of 19 hours in December to a winter minimum of 6 hours in June. The position of Signy Island (as described in chapter 1) close to the northern edge of the Weddell Sea gyre results in large interannual variations being superimposed on the seasonal cycle of seawater temperature, ice cover and chlorophyll standing crop (Murphy *et al.* submitted). The seasonal cycle of temperature, ice cover, chlorophyll and microzooplankton at Signy Island has been described by Clarke *et al.* (1988) and Leakey *et al.* (1994).

Although feeding activity could be observed in bryozoans held in flow-through

aquaria at the research station, it was felt that measurements *in situ* were essential to document the possible influences of sea-ice cover, current and photoperiod. Limitations of time underwater and for analysis of photographic data dictated that a maximum of four species could be studied. Several species of erect cheilostome bryozoans are common in sublittoral waters around Signy Island, but only two are planar (and hence effectively two dimensional) which is virtually essential for the photographic method used. *Alloeflustra tenuis* and *Nematoflustra flagellata* are extremely abundant in depths below about 35 m. They are usually found at the interface between muddy and rocky substrata, and most densely at the point where the angle of the rock face shallows. *Arachnopusia inchoata* is initially an encrusting species, which, having formed a base, may grow out from the substratum to form massive foliaceous colonies up to 1 metre across. *A. inchoata* occurs at all the surveyed depths, but it is particularly abundant on vertical rock faces between 10 m and 30 m, and in terms of distribution and abundance is one of the most successful bryozoans in the waters around Signy Island (Barnes 1995b). The fourth species chosen for study was *Inversiula nutrix*. This common encrusting species dominates shallow (5 m) and disturbed regions.

Figure 8.1

Map of Signy Island showing position of bryozoan study sites (○) and oceanographic stations (●). FC = Factory Cove site, OI = Outer Island site, PR = Powell Rock site, ST = sediment trap station, SW = seawater sampling station



The species chosen for detailed study thus encompass four of the most dominant species, three different growth morphologies and three different habitats. They also provide an opportunity for comparison between two species similar in morphology and habitat (*Alloeflustra tenuis* and *Nematoflustra flagellata*). The study colonies of *A. tenuis* and *N. flagellata* were at 35 m depth at Powell Rock, those of *Arachnopusia inchoata* at 15 m by Outer Island, and those of *Inversiula nutrix* at 5 m in Factory Cove (Fig. 8.1).

Measurement of feeding activity

Twenty colonies of each species, randomly selected from hundreds in each area, were photographed each month using Nikonos II or Nikonos V cameras equipped with extension tubes and twin electronic flashes. This produced approximately life size replication on 35mm transparencies. Slide film was processed on site and projected to enlarge and clarify observations. As is typical of bryozoans, a zonation of feeding activity was apparent in all four study species (and also in other species observed). The zone of most intensive feeding occurred just behind the outer growing margin and zone of zooid differentiation. This zone of most intensive feeding, marked by the maximum number of everted lophophores, varied little within species but did differ in size and position between species. From this zone, the number of lophophores everted decreased substantially towards the colony base and older regions of the colony.

All measurements in the present study were confined to the zone of maximum lophophore feeding activity. Since each photograph might show thousands of zooids, several areas could be counted for each colony. For each colony the number of everted lophophores was counted in up to ten areas, each consisting of 100 zooids (10 x 10). The mean of these values recorded was taken as the feeding activity (expressed as the percentage of lophophores everted) for that colony, although within-colony variance was always very low and hence the difference between the maximum value and the mean of the ten areas examined was very small. The mean value for each species was calculated from twenty colonies each month.

Environmental parameters

Environmental data was provided from a long running programme of oceanographic/seawater monitoring, involving the following: Regular water samples were collected at a fixed station approximately 100 metres north of Small Rock in Borge Bay (SW: Fig. 8.1). At this station the water depth is 25 metres and the water column is well mixed (Clarke *et al.* 1988). Water was collected with a polyethylene NIO pattern bottle, closed by a brass messenger and carrying three mercury-in-glass reversing thermometers. In summer open-water periods samples were taken every 5 or 6 days from a small inflatable boat; in winter samples were taken weekly through a hole cut in the fast-ice.

Temperature was estimated from the mean of three thermometers which were allowed 15 minutes to equilibrate at depth before tripping. Water samples were transferred to the research station immediately after collection. The samples were gently but thoroughly mixed by inversion and triplicate sub-samples fractionated by passage through a succession of filters under gravity, in the dark. The chlorophyll retained on each filter was extracted at 4°C in the dark overnight into chloroform/methanol (Wood 1985) and assayed fluorometrically. This protocol produced estimates of the chlorophyll biomass in three size fractions (Sieburth 1979):

Microplankton:	> 20 μm (essentially colonial forms, chain-forming species and large single diatoms).
Nanoplankton:	2-20 μm (mostly flagellates and small diatoms).
Picoplankton:	0.2-2 μm (very small cells, cyanobacteria and cell fragments).

The type, area and thickness of sea-ice was monitored weekly throughout the two winters of this study (1991, 1992). Sea-ice duration varies from site to site around Signy Island, mainly because of the effect of local topographic and bathymetric factors. For the purposes of this study, sea-ice parameters were recorded separately for Factory Cove (site FC) and inner Borge Bay (sites OI, PR, ST and SW).

Incident solar radiation was recorded close to the research station throughout the study period. The maximum monthly average was 232.5 W m^{-2} in December 1992, and the minimum was 5.4 W m^{-2} in June 1992. Unfortunately safety constraints on underwater time at 40 m depth prevented monitoring of light climate *in situ*. Some data for Borge Bay are given by Gilbert (1991), although these data are for an earlier year when fast-ice conditions were very different.

Results

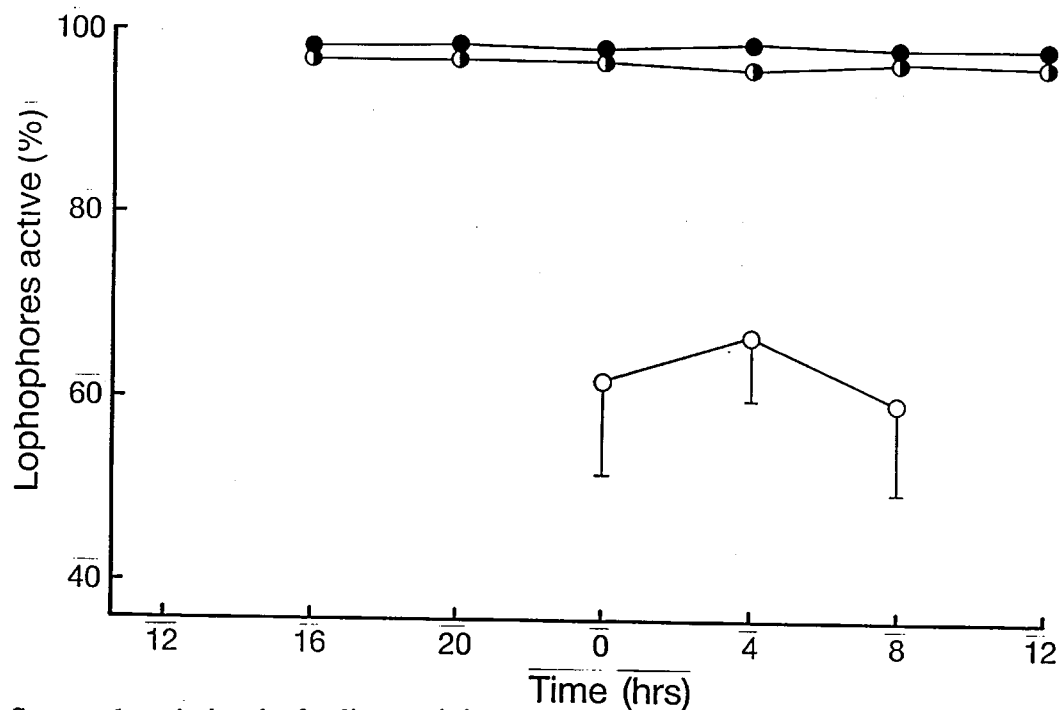
Diurnal variation in feeding activity

Logistic and safety factors dictated that the monthly measurements of bryozoan feeding had to be undertaken during daylight hours. Although much feeding activity in the marine environment takes place by night, laboratory aquarium observations had suggested that there was little difference in the proportion of lophophores extended between night and day. To confirm this observation in the field, thirteen colonies of *Arachnopusia inchoata* and *Beania erecta* were monitored photographically every four hours for a full 24 hour period during November 1992. *Beania erecta* was not included in the main study, but being a common species it could be monitored easily on the same dive as *Arachnopusia*. SCUBA safety considerations limited this study to shallower species and so some extra night observations of *Inversiula nutrix* were made. The results are shown in Fig. 8.2.

Both *Arachnopusia inchoata* and *Beania erecta* fed actively (mean feeding index $>95\%$ lophophores everted) throughout the 24 hour period. The data for *Inversiula nutrix* showed much greater between-colony variance than in either *A. inchoata* or *B. erecta* but in all three species there was no significant variation in feeding activity with time of day (one-way ANOVA, all $P>0.05$). These data indicate that small variations in the timing of the monthly observations will not have resulted in significant error, and that daytime observations will have been representative of feeding activity throughout the 24 hour period.

Figure 8.2

Diurnal variation in feeding activity, as estimated by the percentage of lophophores everted in three species of bryozoan at Signy Island. The species are *Arachnopusia inchoata* (●), *Beania erecta* (◐) and *Inversiula nutrix* (○). Data are presented as mean and standard deviation (n=5 colonies), with the same colonies being visited every 4 hours.

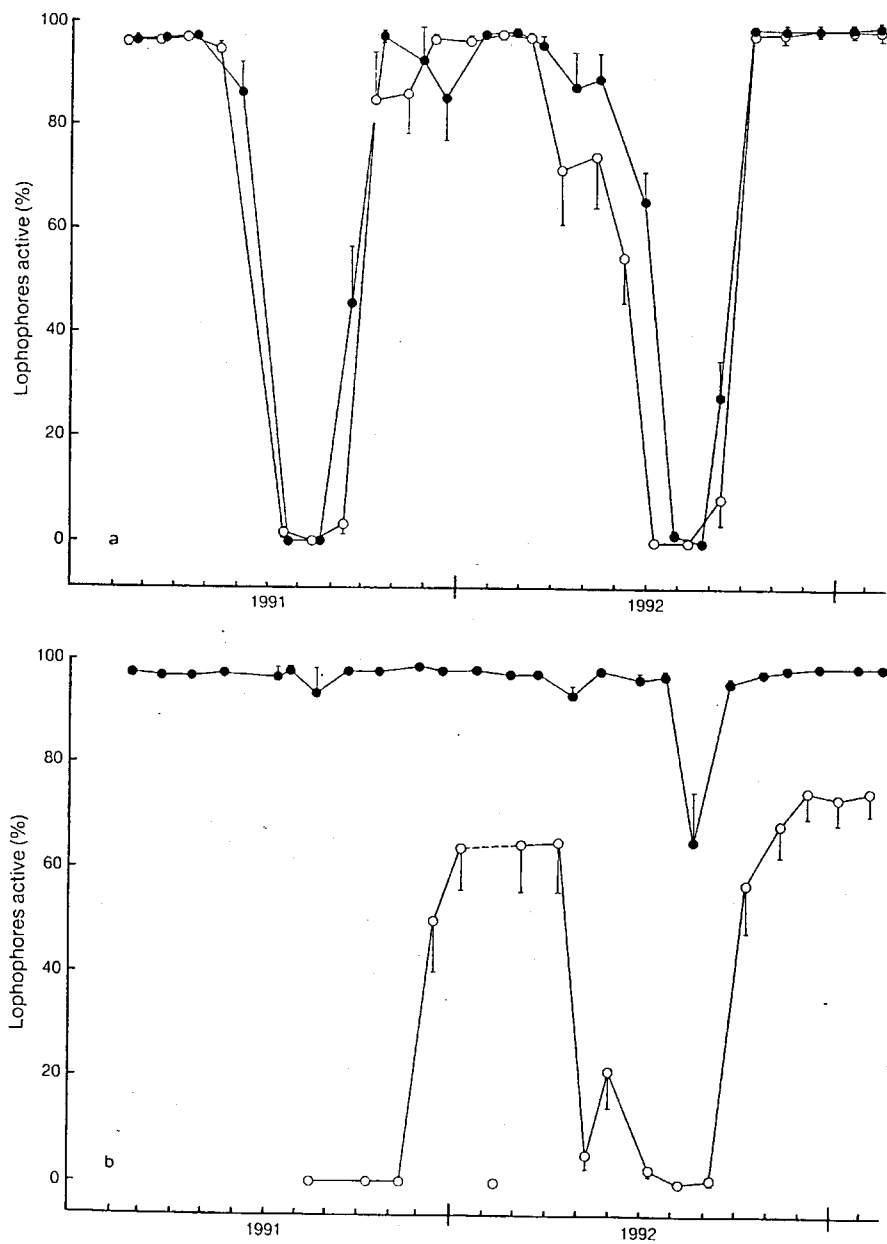


Seasonal variation in feeding activity

The four species studied showed marked differences in the seasonal patterns of feeding activity; they also differed in the extent of between colony variance. The two erect species from deeper water, *Alloeflustra tenuis* and *Nematoflustra flagellata*, showed a clear and very similar seasonal pattern in feeding activity (Fig. 8.3a). Peak feeding activity occurred for at least six months, when the mean lophophore index was 96% or higher. During this time, there was very little variation between colonies. There was then a period of rapid change, when the between-colony variation was very high, leading to a period of zero feeding activity for around three months. During the periods of rapid change in feeding activity of these two flustrids, the between colony variance exceeded that of the stable summer periods in 1990/91 and 1992/93 by a factor of x10. This was the result of differences between individual colonies, rather than variation within colonies. Presumably individual colonies differed in the timing of their response to whatever environmental cue(s) elicit the cessation of feeding activity.

Figure 8.3

Seasonal variation in feeding activity, as estimated by the percentage of lophophores everted, in four species of bryozoans at Signy island. Data are presented as mean and standard deviation for 20 colonies of each species. Note displacement of vertical scale for clarity. (a) Deeper water flustrids: *Alloeflustra tenuis* (○) and *Nematoflustra flagellata* (●). (b) Shallow water species: *Inversiula nutrix* (○) and *Arachnopusia inchoata* (●). One observation of zero feeding activity early in 1992 for *Inversiula* is believed to be an artefact and is therefore not included in the seasonal pattern; the adjoining data points have been joined by an interpolated line (----) (see text).



It is striking that these two flustrid species living alongside one another showed such similar seasonal patterns. Furthermore the sequence of cessation and initiation of feeding activity was also similar between years. In both the 1991 and 1992 austral winters, *Alloeflustra tenuis* ceased feeding slightly before *Nematoflustra flagellata*, and started again later. One further notable feature of the data is that in both species, the 1991/92 summer showed a greater variability in feeding activity than either the preceding or following summer.

The encrusting and encrusting/foliaceous species showed different patterns with respect to the erect species, and to each other (Fig. 8.3b). As with the two erect species, *Inversiula nutrix* spent a number of months over the austral summer with a high percentage of lophophores everted, then changed rapidly to low winter values. It was striking, however, that the mean summer values reached (65-75%) were much lower than in the flustrids, and that between-colony variation is consistently high. In addition, the period of time spent without feeding activity was greater than in either of the erect species. The mean value of zero percent everted lophophores recorded for *I. nutrix* in February 1992 is believed to be an artefact of unusually high current flow (associated with stormy weather). This data point was therefore ignored in deriving the seasonal pattern shown in Figure 8.3b, and an interpolation made between the adjacent data points.

A very different pattern was shown by the massive encrusting/foliaceous *Arachnopusia inchoata* (Fig. 8.3b). With the exception of a short decrease in mid-winter (July), more extensive in 1992 than in 1991, this species maintained a very high level of feeding activity throughout the two year study period. The low value in August 1992 was the result of 5 of the 20 colonies examined showing essentially no lophophore activity. These colonies may have been disturbed prior to photography, possibly by currents.

Three of the four species studied thus showed clear and strong seasonality, with a rapid switch between summer maxima and winter minima. The length of the study period allows comparison between successive years, and subtle differences may be detected. In particular the austral summer 1991/92 showed greater variability in feeding activity in the

two flustrid species. The pattern of the switch from summer feeding to winter non-feeding was also less sharp than in the previous summer (Fig. 8.3a); on day 75 both flustrids were still at peak feeding activity (>95% lophophores everted) but by day 100 the drop to winter levels had started. At the same time *Inversiula nutrix* feeding activity switched rapidly to winter levels, moving from a lophophore index of >65% at day 103 to <10% on day 122 (Fig. 8.3b). In all three species this was followed by a temporary reversal, with feeding activity increasing again in the period from day 135 to 155, before continuing the decline to winter cessation of feeding. These patterns suggest a general response by the suspension feeding community to environmental cues.

Lophophore size

Species may show differences in seasonal patterns of feeding if they are exploiting different resources. In bryozoans some indication of resource utilisation may be obtained from lophophore size. Lophophore diameter and tentacle number for the four species studied are shown in Table 8.1; these data are typical of cheilostome bryozoans (McKinney & Jackson 1991). The two flustrids and *Inversiula nutrix* have similar lophophore diameters but it is not clear whether the larger lophophore of *Arachnopusia inchoata* allows it to exploit a different food resource.

Table 8.1

Tentacle number and lophophore diameter of the four species of bryozoan studied. Data are presented as mean with the standard deviation in brackets. Data were obtained from measurements of fully everted lophophores on life size photographic transparencies of colonies *in situ*.

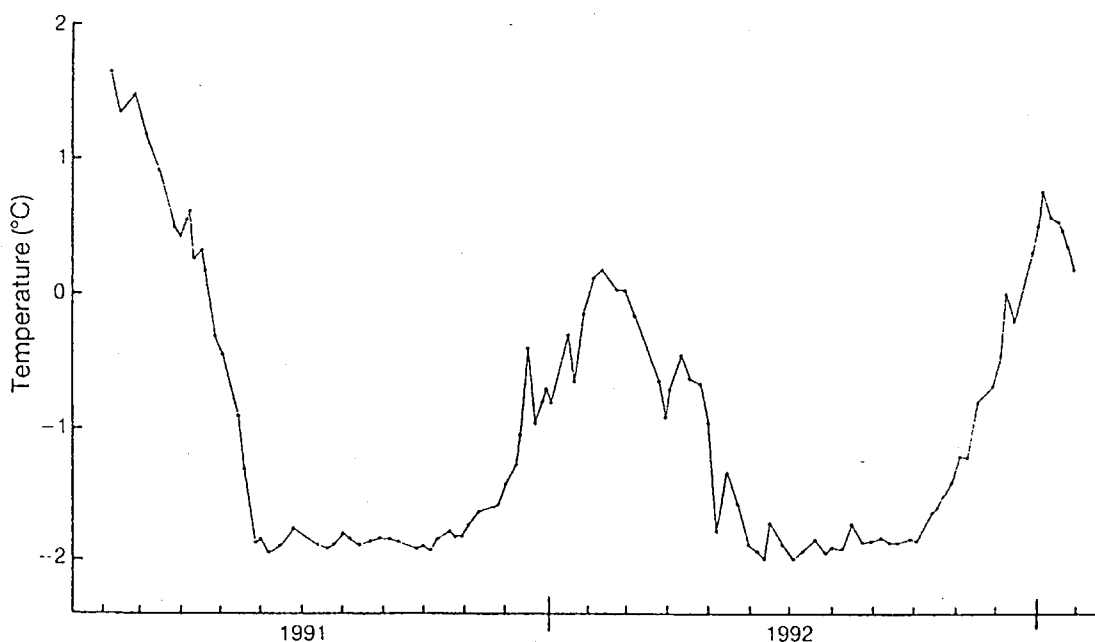
Species	Tentacle number	Lophophore Diameter (µm)	n
<i>Alloeflustra tenuis</i>	15.5 (0.78)	591.7 (0.04)	39
<i>Arachnopusia inchoata</i>	19.4 (0.99)	1013.8 (0.07)	39
<i>Inversiula nutrix</i>	16.0 (0.91)	≈ 800	39
<i>Nematoflustra flagellata</i>	22.4 (0.97)	838.5 (0.04)	37

Seasonal variability in the environment

During the period of this study temperature varied from a summer maximum which differed between the three successive summers, to winter minima of around -1.9°C (Fig. 8.4). The water column in Borge Bay is generally well mixed (Whitaker 1982, Clarke *et al.* 1988) and so these temperatures are representative of those that will have been experienced by the bryozoans in this study. The key features of this pattern are the relatively stable winter minima, the variable summer maxima, and the smooth spring increase and autumn decrease in temperature of approximately $1^{\circ}\text{C}/\text{month}$. Although the annual range in temperature is very small the bryozoans in this study will have been subject to a distinct seasonal variation in seawater temperature.

Figure 8.4

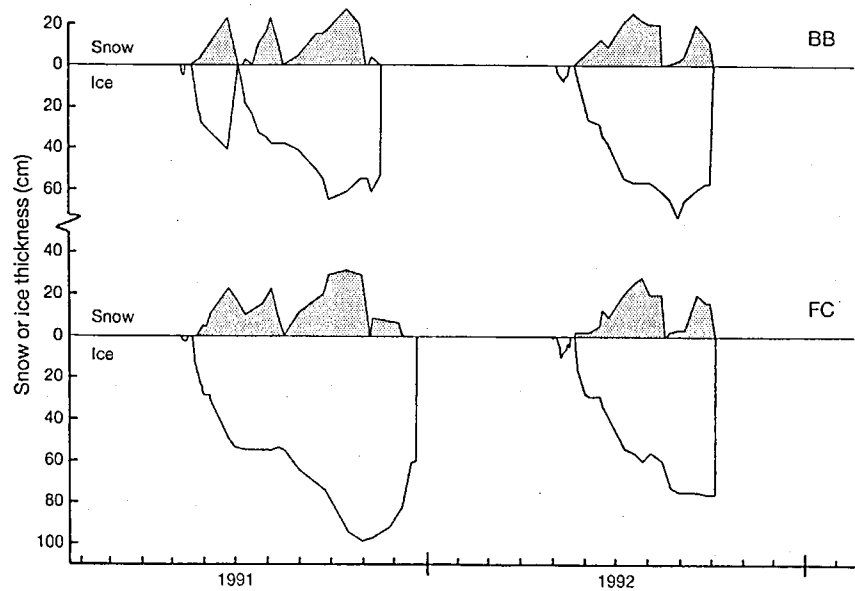
Seasonal variation in seawater temperature recorded at 15 m depth at station SW Borge Bay, 1991-1993. Each point is the mean of 3 simultaneous measurements



Sea-ice formation and break-up is linked to sea temperature and is clearly very seasonal (Fig. 8.5). Many factors also affect sea-ice, and the pattern from year to year may change greatly (Clarke *et al.* 1988, Murphy *et al.* in press). In 1991 and 1992 fast-ice started to form around day 130, grew a little, then disappeared. Embryonic stages of fast-ice, known as grease ice and then pancake ice, are extremely vulnerable to weather conditions and are easily broken up by wind or wave action. Once fast-ice has formed in Factory Cove, its thickness and strength grow steadily, until the air and sea temperatures start to rise in late winter, when both thickness and strength start to decline. Storms may weaken the ice, and may break up the ice cover completely. This is especially likely towards the end of winter, as happened in both 1991 and 1992, which explains the sharp cut off in ice thickness at the end of each season. In both years a strong spring storm resulted in all the local fast-ice blowing out to sea rather than melting *in situ*. Fast-ice closer to the shore tends to be stronger, and hence to last rather longer (see Fig. 8.5).

Figure 8.5

Duration and thickness of winter fast-ice at Signy Island, winter 1991 and 1992. The thickness of overlying snow is also shown (stippled). Data are split into two areas: Factory Cove (FC) close to shore, and inner Borge bay (BB) further out. FC data show the fast-ice cover for the *Inversiula nutrix* site, whereas the inner Borge Bay data show the fast-ice cover for the other three species.

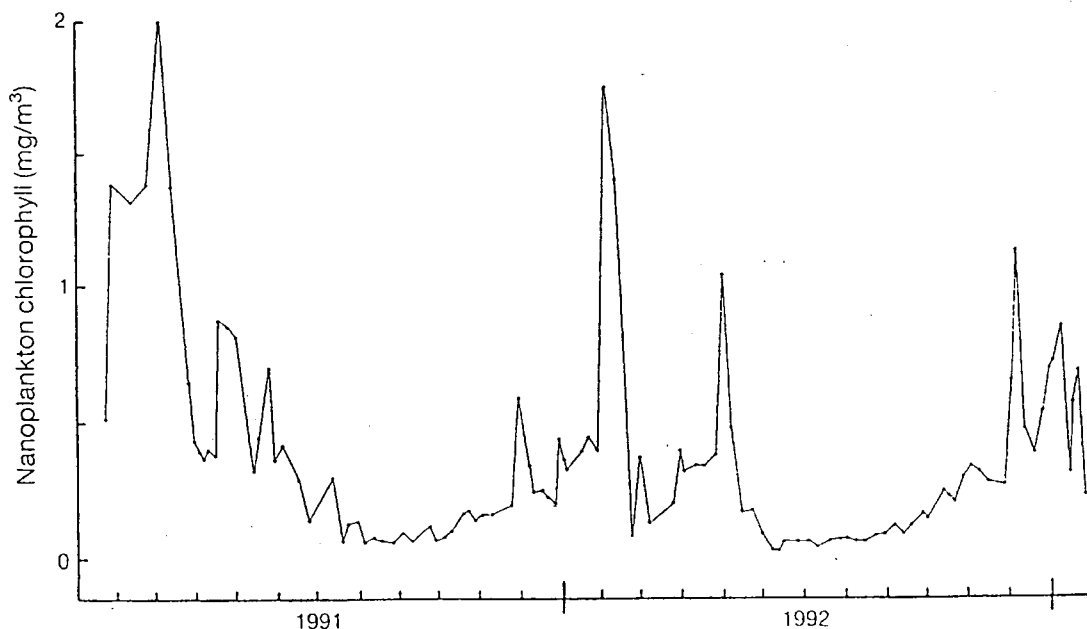


Snow fall may increase the apparent ice thickness, and reduces light transmission (Gilbert 1991), whereas short bouts of warmer weather may induce a series of melts, as happened in both seasons (Fig. 8.5).

The bulk of the phytoplankton production occurs over a very small period of time, around December and January (Whitaker 1982, Clarke *et al.* 1988), but much of this is microplankton and consists of larger diatoms, chains or globular clusters of cells. Bryozoans are believed to feed primarily on smaller diatoms and flagellates (Winston 1977), which are from the nanoplankton. The seasonal variation in nanoplankton chlorophyll during the period of this study is shown in Figure 8.6.

Figure 8.6

Seasonal variation in standing crop of chlorophyll in the nanoplankton fraction (2-20 μm) at 15 m depth at station SW, Borge Bay, 1991-1993. Each point is the mean of three replicate measurements from a single bottle sample. Note displacement of the vertical axis for clarity.



In winter, nanoplankton chlorophyll concentrations were generally between 50 and 100 $\mu\text{g m}^{-3}$, and at the heart of winter (July, August) often exceeded the microplankton chlorophyll concentrations. During spring and early summer nanoplankton chlorophyll increased to

over $300 \mu\text{g m}^{-3}$, with substantial short-term increases superimposed. There were marked differences between the three summer periods of this study. In 1990/91 there was a long-lived nanoplankton bloom which peaked at almost 2 mg m^{-3} . The 1991/92 summer was distinguished by a double bloom in the microplankton (an unusual event at Signy Island: Clarke *et al.* 1988) which was mirrored in the nanoplankton fraction (Fig. 8.6). The early summer bloom peaked at 1.75 mg m^{-3} , whereas the autumn bloom only reached 1 mg m^{-3} . The 1992/93 summer had the smallest bloom of the study. These data emphasise the year-to-year variability in nanoplankton chlorophyll concentration and hence, by inference, food availability for suspension feeders such as bryozoans.

During the period of this study vertical flux of particulate material was measured by a sediment trap array at 10 metres depth. Vertical flux was very low in winter, but increased each summer (Nedwell *et al.* 1993). This pattern matches that reported previously by Gilbert (1991), who also showed that a significant component of this flux is comprised of diatom resting spores. This vertical flux is of profound significance to the infauna (Nedwell *et al.* 1993) but the extent to which it may provide food for suspension feeders is unclear (Whitaker 1981). Usually there is only a single summer peak in chlorophyll flux, but the 1991/92 austral summer was unusual in showing two peaks which matched the unusual double microplankton bloom recorded in that year. The early spring (November 1991) was also marked by a resuspension event when a major storm resulted in bottom sediment being injected into the water column, and subsequently recovered in the sediment traps as it settled.

Discussion

Seasonal variations in feeding activity

This study has revealed a diversity of seasonal patterns of lophophore activity in the four species of bryozoan studied. The two flustrids from deeper water both showed a strong seasonality in lophophore activity, with *Alloeflustra tenuis* ceasing feeding earlier, and

restarting later than sympatric *Nematoflustra flagellata*. The massive encrusting/foliaceous species *Arachnopusia inchoata* differed in showing almost continuous feeding activity, with virtually no sign of seasonal variation. In all three species there was a high degree of synchrony between different individual colonies; between-colony variance was generally low, except during the period of rapid shift from summer to winter levels of feeding activity in the two flustrids. This was not the case for *Inversiula nutrix*, where there was always a high degree of variability between the different colonies being monitored, although this variability did not obscure a distinct seasonality in lophophore activity.

In this study it is assumed implicitly that lophophore eversion is a valid indicator of feeding activity. This is reasonable in that the lophophore is the feeding organ in bryozoans, although the possibility could not be dismissed that there may be times when the lophophore is everted for reasons other than feeding. In the absence of any evidence for non-feeding functions in lophophores, however, it has been assumed that lophophore eversion is indicative of active feeding.

What environmental factors cue feeding?

The marked seasonality of feeding in three of the four study species, and the striking differences between the species, prompt the question of what environmental cues might influence the initiation or cessation of feeding activity. Neither the time nor the facilities for a detailed experimental study were available at Signy Island. The traditional field ecology approach of looking for correlations between changes in feeding activity and environmental variables, was therefore used, taking advantage of the long run of observational data (often on the same individual colonies month after month).

Annual temperature variation at Signy Island is very small and so using the seasonal change in temperature as a cue would imply a high sensitivity. Data from high resolution recorders *in situ* indicate that daily fluctuations in temperature may be high, especially in the summer open-water periods (Clarke unpublished data); this would make detection of a seasonal temperature signal against the daily background noise very difficult.

Temperature seems an unlikely environmental cue because abrupt switches in feeding activity take place whilst the temperature is still at a reasonably constant winter minimum.

Table 8.2

Relationship between the beginning and the end of seasonal feeding activity in the bryozoans *Alloeflustra tenuis*, *Nematoflustra flagellata* and *Inversiula nutrix* in relation to environmental factors at Borge Bay. Data for *Arachnopusia inchoata* are not provided since this species fed throughout the two year study period. The threshold for feeding activity was defined as 75% maximum value (see text). The environmental variables summarised here are temperature (°C), fast-ice (+ present, - absent, with number of days until breakout or formation in brackets), vertical flux (mg chlorophyll m⁻² day⁻¹), nanoplankton and microplankton chlorophyll (both µg m⁻³). ND= no feeding data.

			Environmental variables on date				
			Micro	Nano	Flux	Temp	Ice
<i>Alloeflustra tenuis</i>							
Stop	1991	2 July	156	210	1.8	-1.83	+ (-41)
	1992	26 June	38	40	1.0	-1.93	+ (-52)
Start	1991	10 October	153	91	0.3	-1.85	+ (41)
	1992	5 October	215	158	3.7	-1.78	+ (1)
<i>Nematoflustra flagellata</i>							
Stop	1991	9 July	180	270	1.2	-1.86	+ (-49)
	1992	19 July	54	56	0.4	-1.85	+ (-75)
Start	1991	9 October	172	82	0.3	-1.88	+ (42)
	1992	2 October	180	133	3.2	-1.84	+ (4)
<i>Inversiula nutrix</i>							
Stop	1991	ND					ND
	1992	9 June	87	18	7.0	-1.94	+ (-29)
Start	1991	12 December	1250	240	4.0	-0.78	- (-8)
	1992	8 October	200	150	3.6	-1.181	- (-1)

Sea-ice limits both water movements and light penetration, either of which could be used as cues. The break up of fast-ice is initially a gradual process which may take several days or more; during this process there is a noticeable increase in water movement under the ice. *Inversiula nutrix* commenced feeding 8 days and 1 day before the ice departure in 1991 and 1992, respectively Table 8.2. This species, then, would seem to have the start of summer feeding activity linked to ice break up. The two erect species (*Alloeflustra tenuis* and *Nematoflustra flagellata*) both commenced feeding just before ice break up 1992, but not in 1991. These two species, do however, commence at almost exactly the same time period each year, so photoperiod could not be discounted. None of the three species seems to have cessation of activity linked to sea ice formation. In theory

a sessile benthic organism could detect the break-up of winter sea-ice either by an increase in water movement or a sudden increase in light level (Gilbert 1991). The problem in using the end of winter sea-ice as a cue is that this is a highly variable signal. The duration of fast-ice in Borge Bay can vary from 0 (in 1956) to 219 (1966) days (Clarke *et al.* 1988, Murphy *et al.* in press). Similar arguments obtain to the start of winter sea-ice as a cue to cease feeding; none of the three species studied here with show any evidence of changes in feeding activity being related to sea-ice formation.

The intensity of radiation at the sea-bed is dependent critically on the presence of sea-ice, and particularly of any snow on top of that ice (Gilbert 1991). This will therefore be as variable an environmental signal as sea-ice itself. Photoperiod is a possible cue but this would need experimental verification.

Food availability is more seasonal in the microplankton fraction than the nanoplankton, but the latter is probably most important as food. Between June and September (the austral winter), the concentration of nanoplankton in the water column at Signy is typically 80-100 cells ml⁻¹ (Leakey & Clarke unpublished obs.); peak summer values are typically 1500 cells ml⁻¹. The feeding activity of *Himantozoum antarcticum*, an erect cheilostome which lives in similar areas to *Alloeflustra tenuis* and *Nematoflustra flagellata*, becomes saturated at concentrations of 25000 cells ml⁻¹ and despite being adapted to lower concentrations than typical temperate cheilostomes (Sanderson *et al.* 1994), may cease feeding for 4 months or more (chapter 9). *A. tenuis*, *N. flagellata* and especially *Arachnopusia inchoata*, fed for longer periods, and may be adapted to even lower concentrations of cells.

The environmental data and feeding activity of *Alloeflustra tenuis*, *Nematoflustra flagellata* and *Inversiula nutrix* are summarised in Table 8.2. For numerical comparison the threshold for feeding activity was defined as 75% of the maximum summer levels detected for each species. The date of this threshold was estimated by linear interpolation between adjacent data points. No clear patterns emerge from this summary, and the seasonal pattern of feeding activity in the bryozoans studied show no obvious correlation

with any of the environmental variables measured.

How harsh is the polar winter?

It has long been established that primary production in polar waters is very much more seasonal than in temperate or tropical areas. This has led to the widespread assumption that the polar winter is a period of very low food availability, especially for herbivores (Gruzov 1977, Clarke 1988). This picture would appear to be supported by physiological data for polar zooplankton, many of which produce large overwintering lipid stores (Clarke 1983, Hagen 1988, Clarke & Peck 1991, Hagen *et al.* 1993). It is striking, however, that those few benthic suspension feeders that have been examined do not synthesise overwintering energy reserves (Peck *et al.* 1986a, b, 1987b). This may be related to reduced metabolic costs in benthos compared with plankton (Clarke & Peck 1991).

In conclusion in the maritime Antarctic, at least, the polar winter may not be as harsh for some benthic suspension feeders as has traditionally been envisaged. One bryozoan, *Arachnopusia inchoata*, continues feeding all year round, and three others show only relatively short periods of winter cessation of feeding activity. There is no indication of 'hibernation' (Gruzov 1977) and periods of inactivity are confined to only part of the 'winter' as might be defined from criteria such as temperature or chlorophyll concentration.

Plate 4

Feeding polyps of the hydroid *Tubulopora* sp. surrounded by a demosponge.



Feeding activity: seasonal variability in a range of suspension feeders

Introduction

The annual pattern of feeding duration found in four species of bryozoans, the first *in situ* investigation of Antarctic suspension feeders (chapter 8), diverged strongly from the traditional viewpoint based on the apparent extreme seasonality of the environment. Whilst significant differences were noted between the activity of the four species of bryozoans examined in detail, all were apparently feeding for a substantial period of the year although possible environmental cues to activity changes remained uncertain. The four bryozoans studied were representatives from three broad morphologies, namely encrusting, encrusting massive/ foliaceous and erect. To fully interpret such activity patterns, an understanding must be gained on the degree to which the observations are representative of other bryozoan species within these morphological groups and of other suspension feeding taxa at this location.

This study thus attempted to gain a broad overview of the timing and duration of feeding activity of Antarctic suspension feeders and how much variation there was between different taxa. In order to encompass many more subjects than in the study reported in chapter 8 the degree of detail had to be changed substantially. Several bryozoan species and representatives of some other locally abundant suspension feeding taxa were monitored *in situ* over a two year period. Surprisingly, and despite the intensity of laboratory based feeding work which has taken place particularly at temperate latitudes, to my knowledge no studies similar to the present have been undertaken elsewhere.

Materials and Methods

Study sites

This study was undertaken at sites in Factory Cove (depth 2-6 m), Bare Rock (6-10 m),

Powell Rock (10-26m) and Outer Island (30-45 m) in Borge Bay, close to the British Antarctic Survey research station at Signy Island. The substratum at these sites is mostly vertical rock faces on which a variety of benthic suspension feeders are locally abundant (chapter 2 and 3). The study locations and seasonal cycles of environmental variables have been described in more detail in previous chapters.

Measurement of feeding activity

The feeding activity of representatives from four abundant benthic suspension feeding phyla (holothurians, polychaetes, hydroids and bryozoans) was monitored at Signy Island over the period 1991 - 1993. In these taxa the presence or absence of feeding activity is relatively easy to distinguish in the field, whereas in others (such as sponges or brachiopods) it is not. Although collection of particulate matter could not be observed in the field, it was assumed that bryozoans and hydroids were feeding when the individuals zooids or polyps had their lophophores or tentacles, respectively, everted. Similarly, holothurians (believed to be a species of *Cucumara*) and polychaetes, *Potamilla antarctica* (Sabellidae) and *Spirorbis* sp. (Spirobinidae) were assumed to be feeding actively when their tentacles were everted. The hydroid species monitored probably belonged to the genus *Tubulopora*.

Because of their abundance, variety and ease of identification, a high proportion of the animals surveyed were bryozoans. The bryozoan species selected for monitoring were the most abundant representatives of the three dominant growth morphologies found within the shallow sublittoral, namely encrusting, encrusting massive/foliaceous, and erect flexible (Chapter 3). Many of the phyla and species occurred at more than one site or depth (Table 9.1), thus comparisons could also be made between similar animals at different sites/depths. The range of taxa selected also allowed comparisons of feeding temporal patterns between phyla, and between different morphologies and species of bryozoans.

Each site was visited monthly except when ice or weather conditions prevented SCUBA work. Feeding activity was recorded either photographically or visually, and

twenty or more specimens within each taxon were examined (except in the uncommon bryozoan species *Carbasea ovoidea* of which only nine specimens were located). Feeding was recorded as active when more than half of the specimens surveyed had their feeding apparatus everted. In practice the switch from feeding to non-feeding in all groups took place within a single month, and threshold values anywhere between about 25 and 75% would have given identical seasonal patterns.

Table 9.1

Distribution of taxa within the four sites studied. Presence of the taxon at each site is shown by +.

Taxon	Factory Cove	Bare Rock	Powell Rock	Outer Island
Encrusting bryozoans				
<i>Beania erecta</i>		+	+	
<i>Celleporella bougainvillei</i>	+	+		
<i>Escharoides tridens</i>	+	+		
<i>Inversiula nutrix</i>	+	+		
Foliaceous bryozoans				
<i>Arachnopusia inchoata</i>		+	+	+
<i>Lageneschara lyrulata</i>			+	+
Erect flexible bryozoans				
<i>Carbasea ovoidea</i>	+		+	
<i>Himantozoum antarcticum</i>				+
<i>Alloeflustra tenuis</i>				+
<i>Nematoflustra flagellata</i>				+
Holothurians		+	+	
Polychaetes	+	+	+	
Hydroids	+	+		

Results

Feeding duration and seasonality

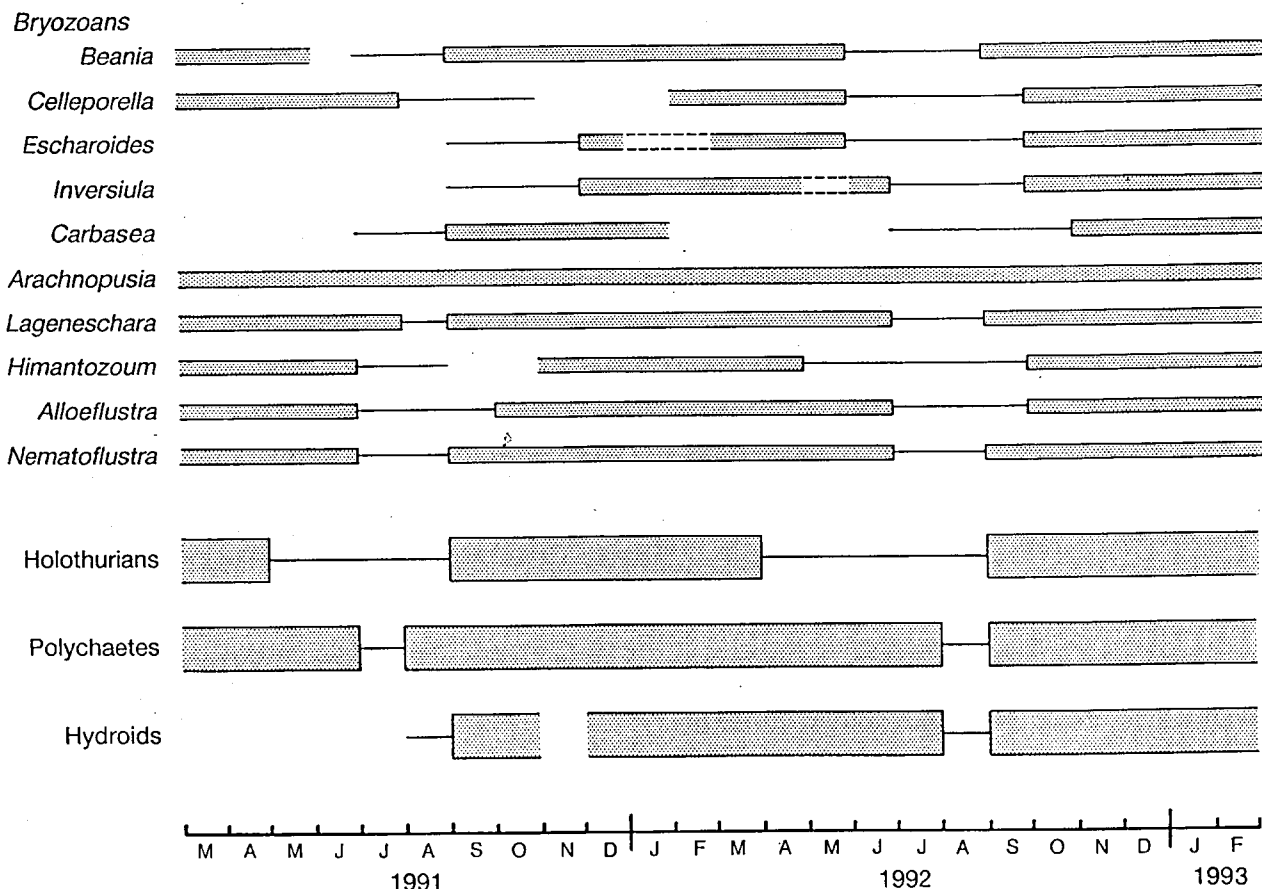
A marked seasonal variation in feeding activity was observed for almost all taxa studied (Fig. 9.1). Most animals ceased feeding for a short period in winter, centred on June and July. The suspension feeding polychaetes (sabellids and spirorbids) monitored, the hydroids and two species of bryozoans ceased feeding for only a few months. The bryozoan *Arachnopusia inchoata* was unique within this study in feeding actively all year,

as recorded in more detail in the previous chapter. In contrast the holothurians and the bryozoan *Himantozoum antarcticum* ceased feeding for as much as five months in winter.

The seasonal pattern of feeding activity was broadly similar in most of the animal taxa studied, although there was a substantial difference between the extreme examples of the bryozoan *Arachnopusia inchoata* and the holothurians. The holothurians usually began feeding at a similar time to the earliest of the other taxa (although in 1991 they were preceded by one month by polychaetes). The difference in the duration of feeding activity of *Himantozoum antarcticum* and the holothurians was caused by a much earlier cessation of feeding (March) in the latter taxon. Whereas the bryozoans showed a variation in feeding activity as great as that across the entire assemblage, the two groups of polychaetes studied (sabellids and spirorbids) were very similar in the overall duration of feeding, and the timing of the initiation and cessation of feeding.

Figure 9.1

Feeding activity (shaded blocks) and inactivity (lines) of various benthic suspension feeders with month of year, for 1991 - 1993. Gaps indicate periods with no data.

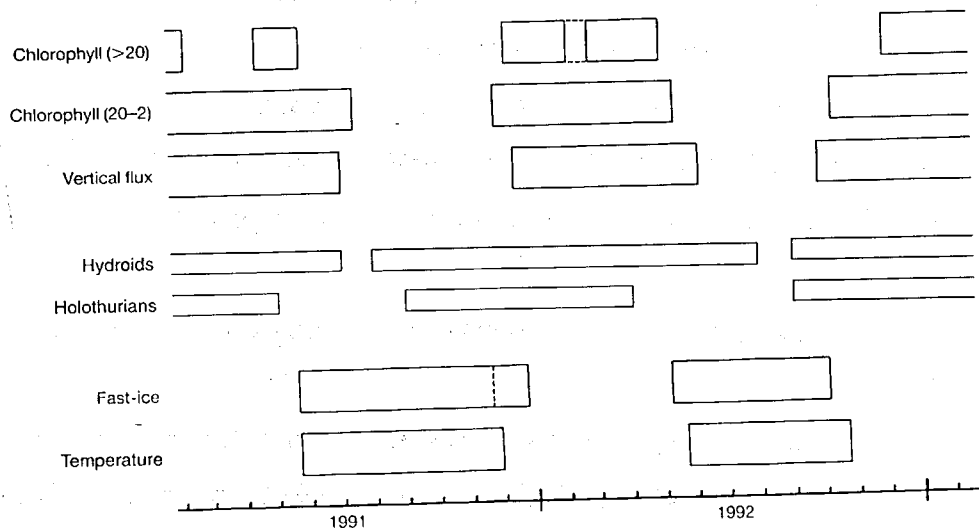


In none of the taxa studied were any differences in the timing of initiation or cessation of feeding noted between sites or depths. Thus, for example, the timing of feeding activity in polychaetes and hydroids was identical at Factory Cove, Bare Rock and Powell Rock. Differences in feeding activity between years were relatively small, particularly with respect to duration. Nevertheless some between year differences in feeding were detected and these, despite being small, may give clues towards those environmental influences which cue changes in feeding activity.

The duration of winter fast ice in outer Borge Bay was greater in 1991 than 1992, but at 203 and 156 days respectively (Figure 9.2) both were above the overall mean of 141 days (Clarke *et al.* 1988). The duration of ice cover over the shallower sites, Bare Rock and Factory Cove, was the same as Borge Bay in 1992, but 35 days longer inshore in 1991.

Figure 9.2

Duration of the diatom and flagellate phytoplankton blooms, fast-ice cover, winter sea temperatures and feeding in polychaetes and holothurians (representing two extremes from fig. 9.1) at Borge Bay, Signy Island. The threshold criteria for the bars were: microchlorophyll (principally diatoms) $>1\text{ mg/m}^3$, nanochlorophyll (principally flagellates) $>200\text{ }\mu\text{g/m}^3$, vertical particle flux $>1\text{ mg/m}^2/\text{day}$, and sea water temperature $< -1.5^\circ\text{C}$. The dotted line within the fast-ice bar represents the earlier breakup of ice in outer Borge Bay, compared with Factory Cove closer to shore.



For all taxa except the holothurians, the periods of zero feeding activity occurred during 'high winter' conditions when fast ice was present, vertical particle flux was very low, and the sea temperature was at the winter minimum of around -1.8°C (Figure 9.2). At this time high resolution temperature records indicate that there was very little water movement beneath the ice (Clarke unpublished data). It was striking, however, that whilst high winter conditions as indicated by these environmental parameters lasted for approximately six months in both years, most taxa ceased feeding for only about three months. Most also commenced feeding in August or September of each year, when few of the environmental factors had changed from 'high winter' conditions.

Discussion

What environmental factors cue changes in feeding activity?

The results of this study showed that the four bryozoan species, for which more detailed observations taken were discussed in chapter 8, seem to be fairly typical of suspension feeders at Signy Island. Changes in the feeding activity of most taxa occurred during the period of winter sea ice and minimal temperature, when the water column was undisturbed and chlorophyll levels and particle flux were also at their lowest. High resolution temperature data indicate that there was a distinct increase in disturbance by currents a few days before fast ice break up (Clarke unpublished data). At the same time there may be changes in water clarity after a long period of minimal disturbance and these changes may act as an a cue for initiation of feeding activity. Some evidence for a disturbance cue is provided by the later start to feeding at the shallow sites compared with deeper sites (see Fig. 9.2). This was noted in the bryozoans *Inversiula nutrix* and *Escharoides tridens*, and may relate to a delay in the break out of fast ice from the shallow near-shore coves.

The close agreement in timing of start of feeding of all taxa in 1992 compared with 1991 may also be indicative of disturbance as a cue since the break up of sea-ice in 1991 was much more gradual than in 1992. Disturbance would reach deeper animals earlier

(being further away from shore) and could proceed sea ice break up through a change in current patterns beneath the winter sea-ice. This may also explain the initiation of feeding before sea ice break up in some taxa.

Photoperiod is also a possible cue, as suggested by the similarity in timing of the start of feeding activity in many taxa between the two years. The light levels reaching the benthos is, however, greatly complicated by the duration of fast-ice and particularly the variation in snow thickness on the fast-ice (Gilbert 1991). The most obvious possibility for an environmental cue is, however, a change in water column chlorophyll concentration.

Since 1989 particulate matter in water samples collected at the Signy Island sampling station have been fractionated into micro (>20 microns), nano (20-2 microns) and pico (2-0.2 microns) size classes prior to chlorophyll assay by fluorometry. In all years the micro fraction (and especially diatoms) dominated the bloom in terms of biomass (Leahey *et al.* 1994). The fraction most utilised by bryozoans, however, is believed to be nanoplankton (Winston 1977, Winston & Heimberg 1988, McKinney 1990). A recent laboratory study of the Antarctic bryozoan *Himantozoum antarcticum* (which was monitored at Signy in this study), showed that this species would collect small cells and could feed at very low cell concentrations (Sanderson *et al.* 1994). Furthermore, a study of another Antarctic bryozoan (*Cellarinella watersi*) revealed a positive correlation between the duration of the summer nanoplankton bloom and the size of the annual growth increment (chapter 10).

Although the nanoplankton bloom is also highly seasonal, the duration of the summer bloom exceeds that of the diatom bloom (Leahey *et al.* 1994, Barnes & Clarke 1994). The timing of cessation of feeding of most taxa matched approximately when nanoplankton concentration reached winter concentrations. The timing of the spring initiation of feeding did not, however, match that of the spring rise in nanoplankton chlorophyll (Fig. 9.2). Holothurians, which ceased feeding earliest in the late summer are believed to feed on the larger cells of the microplankton (Jørgensen 1966, reviewed in Jangoux & Lawrence 1982), which at Signy reached winter (minimal) levels of cell

concentrations earlier than the nanoplankton (Leakey *et al.* 1994). In the austral summers of 1990/1991 and 1991/1992, there were second peaks of microplanktonic abundance after the main bloom (Fig. 9.2). In 1991 the second bloom an unusual early winter diatom bloom which collapsed as winter sea-ice formed. In the following season the apparent double bloom was more likely caused by the arrival in the sampling area of a different water mass of higher chlorophyll concentration; this extended the duration of the summer bloom into the autumn. In neither case did the unusually large duration of high diatom cell counts result in continued feeding activity by holothurians (Fig. 9.2). The apparent lack of response by the holothurians to these second peaks of phytoplankton abundance suggests that either the presence of food alone is not a sufficient cue, or that they are unable to respond to short periods of enhanced food availability. The overall conclusion is that it is most likely that a combination of cues are used for feeding activity, or there are different cues for initiation and cessation.

How can polar benthic suspension feeders feed for so much of the year?

Bryozoans are thought to feed chiefly on the nanoplankton (Winston 1977, Winston & Heimberg 1988), and the feeding rate of the only Antarctic bryozoan studied to date has been shown to be most efficient at low cell concentrations (Sanderson *et al.* 1994). Thus, despite the brevity of the summer peak in diatom cell numbers, the levels of nanoplankton occurring throughout much of the year may be sufficient for many benthic suspension feeders. The basal metabolic costs of these organisms in polar regions may be very low (Peck *et al.* 1987) and this will also benefit those species able to utilise low food concentrations.

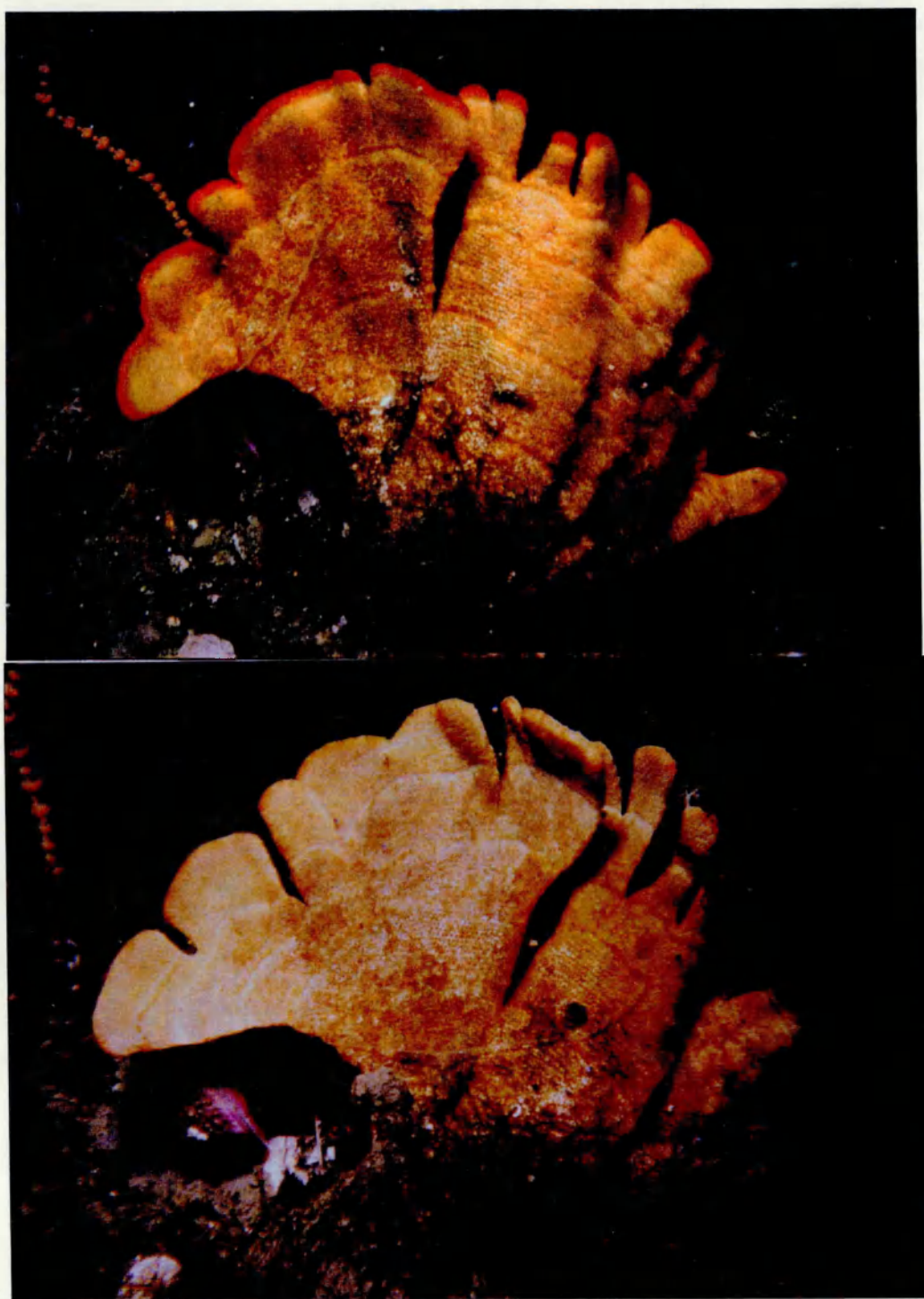
It is likely that different species will feed most effectively on different size fractions of phytoplankton and have different feeding thresholds. This would then translate into differences in the temporal pattern of feeding activity. A few species, possibly *Cellarinella watersi* may only feed and grow for a short period (chapter 10), utilising only the brief summer diatom bloom, but most of the animals studied feed for periods of time comparable with equivalent temperate species.

These observations, coupled with the more detailed study of four bryozoan species discussed in chapter 8, suggest that we need to revise our ideas of a harsh polar winter, at least for the benthos. Rather than being a long period characterised by darkness and inactivity (or even 'hibernation'), winter is a period during which most polar suspension feeders are able to feed actively for all except two or three months centred on July. Photoperiod and incident illumination are dictated by latitude (60°S), although winter ice and especially overlying snow may severely reduce the light reaching the benthos. Despite the short photoperiod, low light level and the very stable water column, there are nevertheless cells present (Leahey *et al.* 1994) and these may be available to species with low feeding thresholds. Recent observations have also suggested that when ice is not present, wind or wave driven resuspension may allow benthic suspension feeders to utilise benthic microflora as food (Ahn 1993).

The general lack of large overwintering lipid store in polar benthos (Clarke 1983, Clarke & Peck 1991) indicates that energy demands and energy availability are broadly in balance. These data suggest that as well as the low resting metabolic rate (Clarke & Peck 1991) winter food, albeit at a low level, may be an important factor. It is not clear to what extent these conclusions may apply to benthic communities living in high Antarctic regions.

Plate 5

Two photographs of a colony of *Cellarinella watersi* taken exactly a year apart.



Seasonal and annual growth in erect species of Antarctic bryozoans

Introduction

The growth of polar marine organisms has been widely studied over the past 15 years, particularly in relation to the growth of related species from warmer water. Recent work has indicated that when invertebrates of like size and ecology are compared, the annual growth rate of polar species is generally slower (Everson 1977, Ralph & Maxwell 1977, Clarke 1980, 1983, Luxmoore 1982, Arntz *et al.* 1994). Growth rates are, however, quite variable and a small number of taxa, notably two sponges; *Mycale acerata* and *Homaxinella balfourensis* (Dayton *et al.* 1974, Dayton 1989) and the ascidians *Ascidia challengerii*, *Cnemidocarpa verrucosa* and *Molgula pedunculata* (Rauschert 1991), have been shown to grow relatively quickly. Where growth has been monitored throughout the year, most appears to take place during the brief polar summer period (Clarke & Lakhani 1979, Richardson 1979), and growth rates during this period may be comparable with temperate species (Nolan & Clarke 1993, Peck & Bullough 1993). Overall annual growth rates are, however, usually reduced because of slow or nonexistent growth in winter. To date, growth studies of polar marine invertebrates have concentrated on unitary organisms, although both direct observation (White & Robins 1972, Barnes 1995 a,b), trawling (Winston 1983, Winston & Heimberg 1988) and remote photography (Bullivant 1961, 1967) have shown that large areas of benthos are dominated by colonial suspension feeders. In order to obtain a balanced perspective of growth in polar latitudes, it is important that suspension feeders are examined.

Recent work on bryozoan growth at temperate latitudes has concentrated on encrusting species (Lidgard 1985, Cancino & Hughes 1987, Rubin 1987, Silén 1987, Lidgard & Jackson 1989). An early study, however, examined the erect temperate species *Flustra foliacea* (Stebbing 1971), and demonstrated clear check lines separating each year's growth. This check was shown to be caused by a period of zero or reduced growth over the winter period. Trawled specimens of rigid erect Antarctic bryozoans of the family Cellarinellidae showed similar lines, which led Ryland (1976) to suggest these might also

be annual growth checks. Winston (1983) further postulated that the variation in width of the internodes between checks may reflect years of high and low food availability.

During the winter period, food availability for many species is low. This has led to winter being viewed as a period of starvation (Clarke 1988, Fenchel 1990) or even 'hibernation' (Gruzov 1977) for polar benthic organisms. The previous two chapters have, however, revealed that many suspension feeding taxa including most of the bryozoans studied are active for most of the year, suggesting that winter starvation may not be as severe as previously thought (Barnes & Clarke 1994, 1995a).

In this study the growth *in situ* of two erect species of cheilostome Bryozoa was monitored using inserted tags and natural growth check lines. Measurements were made between 1991 and 1993, as part of a broad study of Antarctic inshore bryozoan ecology. The aims of the study were threefold: to see whether growth in polar bryozoans varied between summer and winter, to compare growth rates of two polar species with different morphologies, and to compare polar growth rates with those of temperate species.

Materials and methods

Study site and species

This study took place at Outer Island and Owens Bank in Borge Bay. The two sites are both on shallow slopes at depths of approximately 40 m, and characterised by a thin layer of silt overlying rock rubble with a few small (0.5-1.5 m) rock faces protruding. These two sites were also used for the collection of rocks for the investigation of competition and colonisation amongst benthos, described in chapter 4.

It was felt essential that measurements should be made *in situ* (as with the study of feeding described in the previous two chapters) so as to allow comparison with simultaneous measures of environmental variables such as food availability, sea ice cover

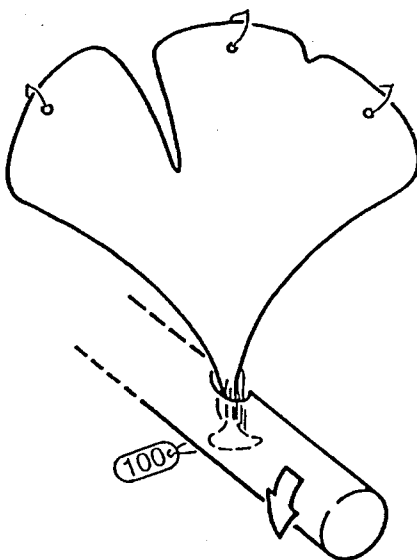
(affecting current and light regimes) and temperature. Operational constraints, including SCUBA underwater time and photographic considerations, together with the requirement to remove specimens later for measurements of mass, suggested that planar erect species would be most suitable for study. Only two erect planar species are common in the sublittoral at Signy Island: *Alloeflustra tenuis* and *Nematoflustra flagellata*. Like *Flustra foliacea* (Stebbing 1971, Silén 1981), each of these two species grow as a unilaminar fan-shaped sheet from an encrusting base, but differs in developing supportive kenozooidal "rootlets". A third species, *Cellarinella watersi*, could be found in only one locality accessible to SCUBA but is common in deeper (>50 m) water. *C. watersi* differs from the two flexible 'frond-like' species in being fully rooted, bilaminar and having a rigid, heavily calcified form. *C. watersi* was chosen for comparison with the flustrid species and also for investigation of the distinct growth checks described by Winston (1983).

Measurement of growth

The growth of *Alloeflustra tenuis* was monitored over the years 1992 and 1993. Twenty specimens of *A. tenuis* were collected from 40 m depth at Outer Island and kept submerged at ambient water temperature in aquaria. These had small (0.5 mm diameter) twine tags inserted just behind the growing margin in five of their many 'branches'. The distance from these tags to the margin was then measured by eyepiece micrometer using a binocular dissecting microscope suspended over a small 'flow through' aquarium. These tagged specimens were mounted on a hollow rod (Fig. 10.1), which was clipped on to a base and positioned in an area containing many (unmarked) colonies, at 40 m depth. At selected times the tagged specimens were recovered and all the epifauna was removed using a scalpel.

Figure 10.1

Tagged and mounted *Alloeflustra tenuis* specimen



The distance from the tags to the 'branch' margins was measured to derive the growth increment, which was then cut off. After 48 hours at 60°C, a dry mass measurement was made for the specimen minus the excised growth increment, the growth increment itself, and all epibiota. These were then ashed in a furnace at 550°C for 12 hours, dried and reweighed to obtain an estimate of organic matter (ash-free dry mass).

Nematoflustra flagellata is similar to *Alloeflustra tenuis* and is found in similar habitats. The growth of tagged individuals was monitored during the austral summer period of 1992-1993. *N. flagellata* was used as a comparison because the two flustrid species have similar growth forms, habitats and feeding behaviour (chapters 8 & 9).

Twenty specimens of the calcareous erect species, *Cellarinella watersi* were monitored by photography every two months for 18 months, to determine whether the growth checks were produced in a specific period of time. A Nikonos II camera equipped with extension tubes and twin electronic flashes was used to obtain 35mm transparencies. These were developed on site and enlarged by projection to clarify observations. At the end of the study 19 specimens were collected (10 from the monitored site and 9 from the nearby vicinity), and carefully separated into their component rings. Dry mass and ash-free dry mass measurements were then obtained on the component rings, using the same method as with *Alloeflustra tenuis*. Counts of the numbers of zooids were also made for each band, along with 5 specimens from photographs taken *in situ*, but which were not collected.

Results

Growth of *Alloeflustra tenuis*

The two flustrid species studied showed very different patterns of growth. *Alloeflustra tenuis* specimens were recovered, tagged and replaced during May and October 1992, when planktonic food was at its stable winter minimum. Growth during the winter period was slightly slower than that of the two summer periods analysed (Fig. 10.2), but not

significantly so (ANCOVA, $P = 0.316$). It is possible that a very brief cessation of growth occurred within the winter period (dotted line Fig. 10.2), obscured by the timing of the measurements. Despite the seasonality of feeding data, a cessation of growth is unlikely to have occurred, for two reasons. First; it would be likely to leave check marks such as are seen in *Flustra foliacea* (Stebbing 1971) or the Cellarinellidae (Winston 1983). Secondly, overall growth during the winter period was not significantly different from that during summer. Thus a period of reduced growth for any duration would have to be matched by a similar period of increased growth during that same winter period. Food abundance at this period was uniformly low, so periods of intense feeding and growth seem unlikely. Thus there would appear to be little or no seasonality of growth in this species.

Growth measurements for *Nematoflustra flagellata* were recorded during one summer only. These were around 3.5 to 4 times higher, in terms of total colony dry mass, than in *Alloeflustra tenuis* (Fig. 10.3). It is not known whether this species displays seasonality of growth or growth rate. In terms of feeding activity and other aspects of known ecology, *N. flagellata* and *A. tenuis* are similar, so it may also grow year-round.

The growth of *Alloeflustra tenuis* was monitored over an 18 month period of two austral summers and the intervening winter. Using the logarithmic relationship between initial size and increment (Fig. 10.3), a growth model can be constructed for *A. tenuis*.

Figure 10.2

Annual growth of *Alloeflustra tenuis*, with respect to feeding. Growth data presented from model (using >50 specimens), dashed line represents an alternative interpretation (see text). Feeding data from chapter 8 (Barnes & Clarke, 1994).

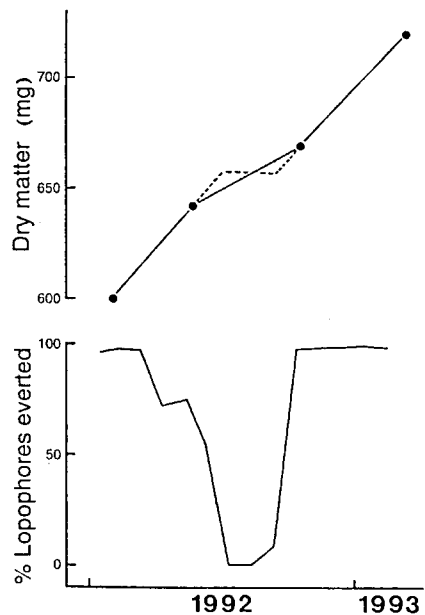
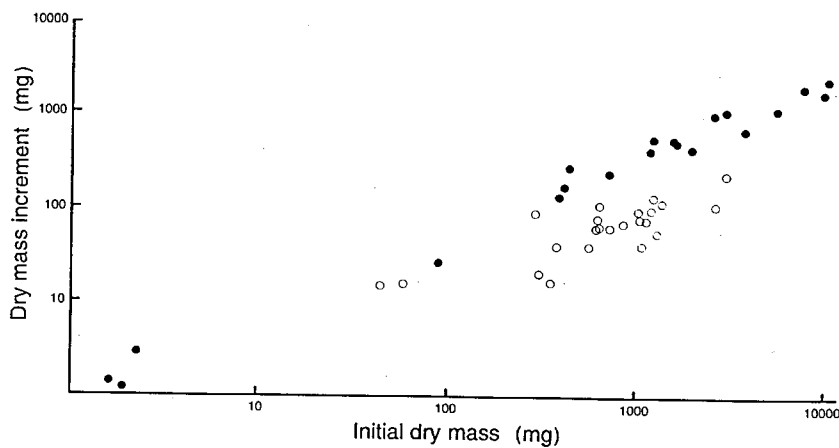


Figure 10.3

Growth, in \log_{10} dry mass, of two erect species of bryozoans, over 1992-1993 summer. The species are *Alloeflustra tenuis* (○) and *Nematoflustra flagellata* (●). Data are presented as individual specimens.



This model suggests that the largest specimens are about 26 years old. Figure 10.2 illustrates the model solved for an individual starting in 1992 at 600 mg dry mass. Unlike *Flustra foliacea* (Stebbing 1971) annual growth check lines are not discernable in *A. tenuis*. Faint growth lines can sometimes be seen towards the growing margin, but these may reflect changes in food availability, and so may not necessarily be annual. The largest specimens of *Nematoflustra flagellata* are three times larger than *A. tenuis* (Fig. 10.3). Since *N. flagellata* appears to grow three times faster during the summer period, the largest specimens may be of the same approximate age as the largest specimens of *A. tenuis*.

Growth of *Cellarinella watersi*

Unlike the two flustrids, the calcareous *Cellarinella watersi* showed distinct growth checks. Photographic monitoring showed that growth (and feeding) ceased in August, September and October. Growth commenced (together with feeding) in November, leaving a conspicuous check line (Fig. 10.4 and plate 5), which was shown to be annual over the 18 month period monitored. The presence of an unusual double peak in phytoplankton, as occurred in the summer of 1991-1992, may leave a fainter check line within the year. *C. watersi*, in contrast to *Alloeflustra tenuis*, thus exhibits a distinct seasonality in growth.

Assuming all major growth bands in *Cellarinella watersi* to be annual indicates that the oldest specimens at this location were 9 years old. Rooted bryozoans, including *C. watersi* are characteristic of deep water locations, and the Owens Bank site is at the shallow end of the distribution of this species at Signy Island. Mechanical damage, almost certainly from currents, was observed in a number of specimens, as has been reported for other species of Cellarinellidae (Winston 1983). With the exception of a couple of specimens from a sheltered position, the maximum height of specimens at the Signy sampling site was similar, regardless of age (Fig. 10.5). It appears that growth in excess of about 5cm results in a high probability of mechanical skeletal damage (presumably by water currents). Colonies usually break along one or more of the growth check lines, where the skeleton is thinnest and which are consequently the weak links. Such damage may take the form of material growth above 5cm being broken off, as seen in some specimens (marked *, Fig. 10.5), or the entire individual breaking off at the base (marked ▲, Fig. 10.5). Colonies growing with perpendicular branches must, therefore, greatly increase their chance of branch loss or damage through catastrophic current resistance.

Figure 10.4

Colony of *Cellarinella watersi* in 1991 (left) and 1992 (right), showing the formation of a growth check line. The shaded band represents the material grown during the 1990/1991 austral summer.

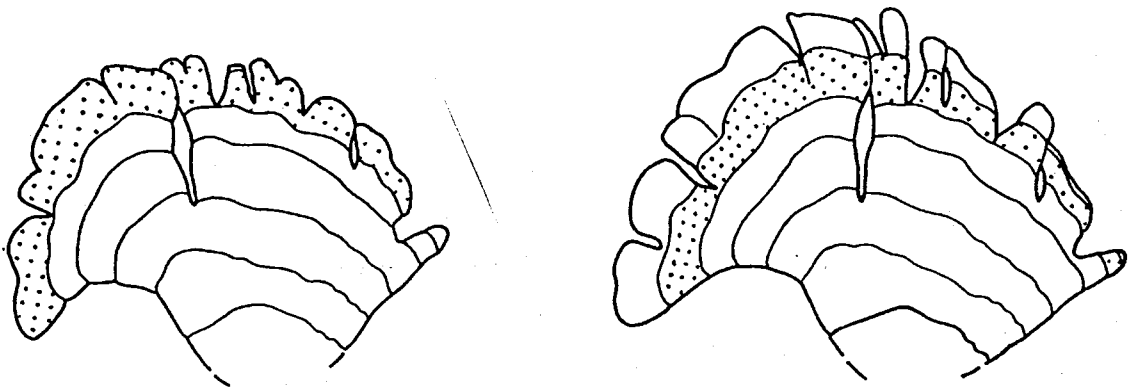


Figure 10.5

Variation in morphology and damage in specimens of *Cellarinella watersi* from Owens Bank site, Signy Island. Specimens marked with a * denotes those with colony branch tops broken off, and those marked with a ▲ have broken off at the colony base.

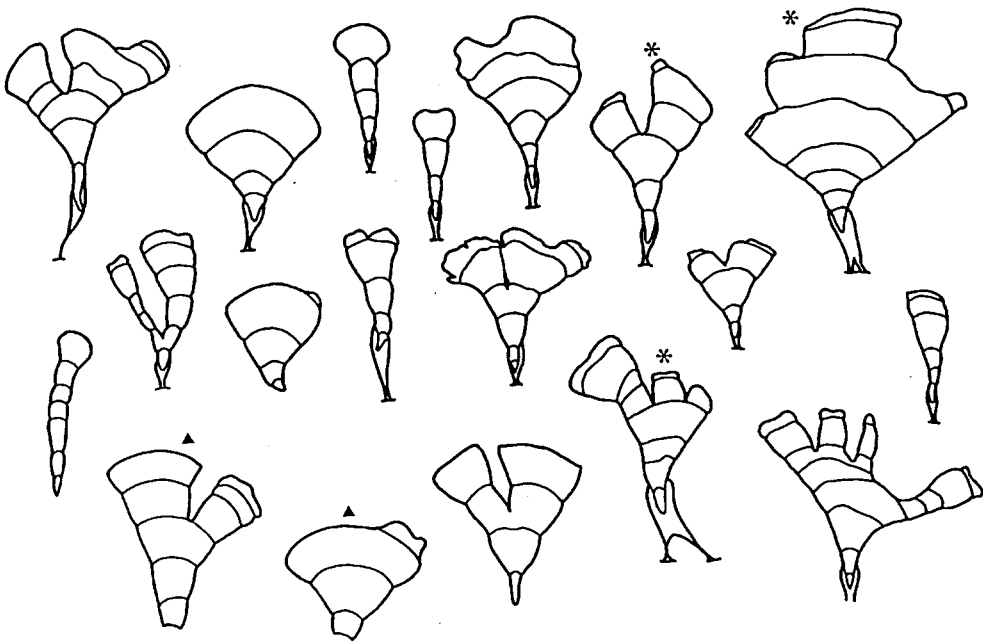


Figure 10.6

Colony of *Cellarinella watersi* showing growth in one (left) arm following breakage of the right arm).

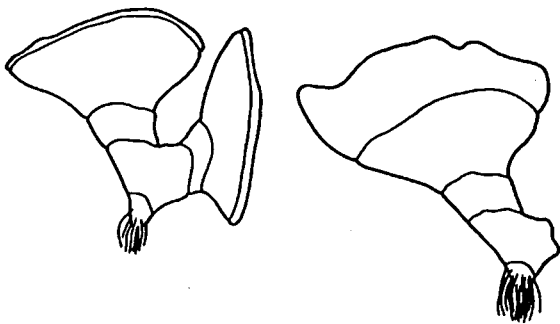


Figure 10.6 illustrates a colony with perpendicular branches, monitored in 1991 and 1992. The fallen piece resulting from the fracture (Fig. 10.6) began to form rootlets (as was also observed by Winston 1983). Growth from fragments was also found in another species, *Cellarinella nutti*, trawled from deeper water. The position of the root complex in one specimen suggests that self-righting is possible using rootlets.

In *Cellarinella watersi* growth, in terms of zooid production, slows with age after 4 years (Fig. 10.7a). This differs from the continuous logarithmic growth observed in *Flustra foliacea* (Stebbing, 1971) over 7 years. In this way growth is substantially lower than *F. foliacea*, by a factor of about twenty (Table 10.1). To some extent this might be expected as a result of the higher energetic costs in *Cellarinella watersi* caused by a greater skeletal calcification (Palmer 1981).

Table 10.1

Annual growth in *Cellarinella watersi* and *Flustra foliacea* in terms of mean zooidal increment, with age. The data for *Flustra foliacea* are taken from Stebbing 1971.

Age / years	Growth in mean number of zooids	
	<i>Cellarinella watersi</i>	<i>Flustra foliacea</i>
1	43	600
2	142	4000
3	309	9500
4	640	25000
5	876	52000

The ratio of dry mass to zooid number in *Cellarinella watersi* decreases linearly with age (Fig. 10.7a). In terms of dry mass however, *Cellarinella watersi* grows only slightly less annually (in the first four years) than the temperate species *Flustra foliacea* (Stebbing 1971). The growth rate of the fastest growing individuals of *C. watersi* would be well above the mean growth for *F. foliacea*, for a given year within this period.

Figure 10.7a

Growth in *Cellarinella watersi*: zooid number as a function of age. Data presented as mean and standard error ($n \approx 20$, for years 1-5; $n = 5$, for years 6 & 7); note logarithmic axis. Ratio of dry mass to zooid number of *Cellarinella watersi*, with age in years. Data presented as mean and standard error (years: year 1, predicted value to exclude mass of root complex).

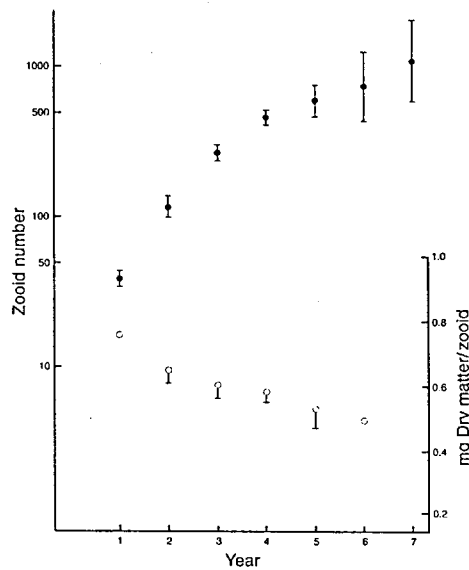


Figure 10.7b

Annual growth in dry mass, of two different types of erect Bryozoa, with time in years. The species are *Alloeflustra tenuis* (○) and *Cellarinella watersi* (●). The data are presented as mean and standard error (15 for *C. watersi* and from model (using >50 specimens) for *A. tenuis*. Note loga

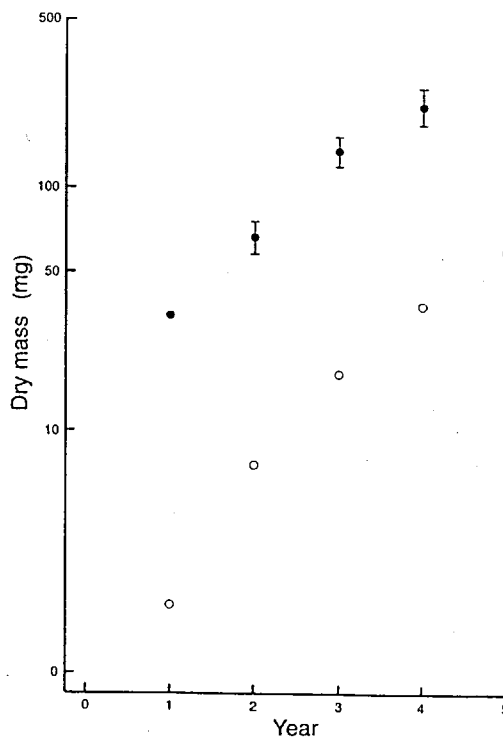
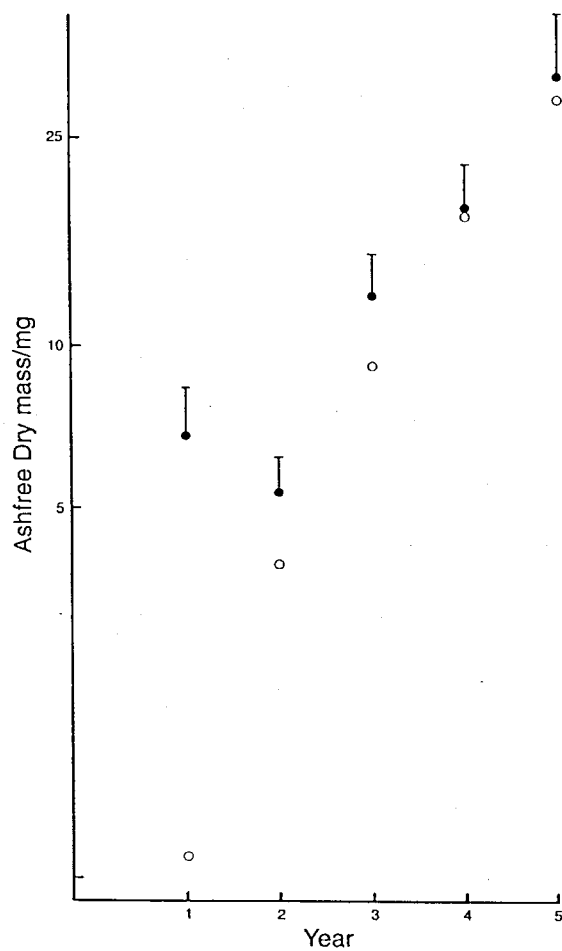


Figure 10.7c

Annual growth, ash-free dry mass, of two different types of erect Bryozoa. Species are *Alloeflustra tenuis* (○) and *Cellarinella watersi* (●). Data are presented as mean and standard errors (n = 15) for *C. watersi* and from model (using >50 specimens) for *A. tenuis*. Note logarithmic axis.



When measured in terms of ash-free dry mass, the pattern of growth differed slightly from that of dry mass. The first year's growth shows a relatively high organic content, probably as a result of the development of the rootlet system. This rootlet support may continue growing after the first year, but could not be distinguished from true first year growth. This produces a small error in measurement of organic growth, resulting in a slightly raised organic content for first year growth, and consequently lowered for the second. With the exception of the first year, the values of ash-free dry mass growth are similar in *Cellarinella watersi* and *Alloeflustra tenuis* (Fig. 10.7c). These values must be substantially lower than those of the temperate species *Flustra foliacea*, although Stebbing (1971) did not provide organic/ ash-free dry mass data to allow a direct comparison.

Annual variation of growth in *Cellarinella watersi*

In order to investigate differences in growth rate between years, the effect of age on growth rate must be taken into account. Although the data set spans 8 years, only four years have a sufficiently large number of measurements for analysis. Thus despite one colony being nine years old, sufficient data (>5 data points for a given growth band) were available only for bands laid down between 1987 and 1990. Because the number of zooids laid down each year increases approximately logarithmically, growth was expressed as the logarithm of the ratio of the number of zooids in a band to the number in the previous band. Analysis of covariance indicated that the relationships between growth rate (= log zooid ratio) and band number were significantly different in elevation ($F = 4.06$, $P = 0.01$) between years. The growth rates achieved by colonies of *Cellarinella watersi* in a given year was therefore expressed as the adjusted means for each year (Table 10.2).

Table 10.2

Growth rate of *Cellarinella watersi* is expressed as the adjusted means from analysis of covariance of log ratio (see text) in band zooid number, for each year separately.

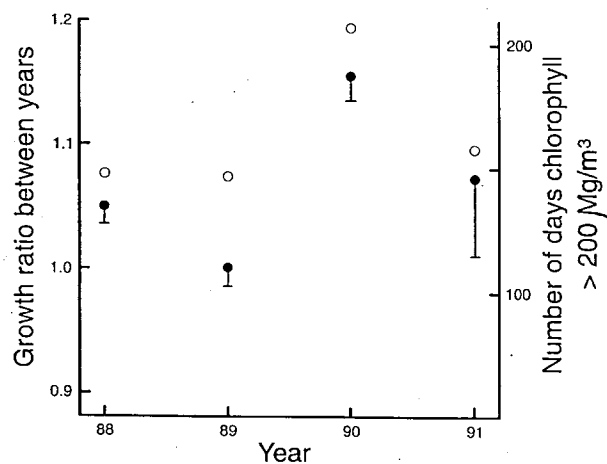
Year	Growth (between year log ratio)	
	Mean	Standard error
1987	0.839	0.021
1988	1.097	0.015
1989	1.025	0.015
1990	1.264	0.021

Regular water sampling at Signy Island has defined the seasonal and interannual variation in the peak biomass and duration of water column phytoplankton production (Whitaker 1982, Clarke *et al.* 1988, Leakey *et al.* 1994). Some Antarctic bryozoans have been shown to feed for much of the year (chapter 8) even when food concentrations are low. Antarctic bryozoans may be able to feed most efficiently at relatively low cell concentrations and also become saturated at low chlorophyll levels (Sanderson *et al.* 1994). This would suggest that the overall duration of chlorophyll abundance would be of more importance to bryozoan growth than the intensity of the bloom. The biomass and duration

of the nanoplankton (2-20 μm) fraction might be expected to relate most closely to bryozoan growth, as bryozoans are believed to principally capture this size range of particles (Winston 1977, Winston & Heimberg 1988). The duration of the nanoplankton abundance shows a close relationship with yearly growth, during the period for which data are available on the growth of *Cellarinella watersi* and the nanoplankton abundance (Fig. 10.8). The duration and intensity of the microplankton ($>20\ \mu\text{m}$) fraction, however, seems completely unrelated to growth of *C. watersi* (Two way ANOVA, $P>0.05$). Unfortunately the plankton sampling at Signy was not size fractionated in 1987, the year for which the growth bands of those *C. watersi* individuals examined showed unusually poor growth (Table 10.2). Thus the nanoplankton duration of abundance is unknown locally for 1987.

Figure 10.8

Growth in *Cellarinella watersi* (●) adjusted means and (○) number of days that chlorophyll in the nanoplankton $>200\ \mu\text{g}/\text{m}^3$.



The influence of epizoites, disturbance and predation on growth

Alloeflustra tenuis and *Nematoflustra flagellata* are both commonly encrusted with epizoites, as previously noted on *Flustra foliacea* (Stebbing 1971). These are principally encrusting cheilostome bryozoans but also include many other taxa (chapter 6). These epizoites may cover large areas of fronds, preventing many zooids from feeding, or weighing fronds down such that the colony might be less competitive for suspended food particles. Stebbing (1971) found that the annual mean increment in colony height in *F.*

foliacea was halved by the presence of such epizoites. Constraints of underwater time precluded the collection at Signy Island of the large numbers of specimens required to test for this effect fully. No significant effect of epizoite intensity on growth was, however, found for either *A. tenuis* or *N. flagellata* after examination of just over twenty specimens of each species. Of the twenty five specimens of *Cellarinella watersi*, none had any encrusting epizoites, although a single specimen from deeper water was half covered by the encrusting/foliaceous cheilostome bryozoan *Lageneschara lyrulata*.

Iceberg activity can be a major disturbance for benthic communities on hard and soft substrata at Signy Island (Peck & Bullough 1993, Barnes 1995 a,b). Observation of the effects of an iceberg impact at a site dominated by *Alloeflustra tenuis* and *Nematoflustra flagellata* showed that almost all of the animals were completely removed over an area in excess of 10 m² (pers. obs.). The age of the oldest specimens indicates that the frequency of scour in these regions may be less than once each 20 years.

No predation or potential predators were noted amongst specimens of *Cellarinella watersi*, though damaged regions were sometimes found on *Alloeflustra tenuis*. In these regions only the calcareous base remains of each zooid. As with holes made artificially (for tagging), regenerative repair takes place from the basal or older end of the damaged region, growing forwards and occasionally forming a new growth margin. Whilst a degree of predation by nudibranch molluscs has been noted on some bryozoans (see chapter 11), predation did not appear to be a major factor influencing growth of the three erect species examined in the present study.

Discussion

Of the two species studied for 18 months, one (*Cellarinella watersi*) exhibited distinct seasonality of growth and left annual growth checks marking changes, and the other (*Alloeflustra tenuis*) grew more or less continually throughout the year. The similarity of *Nematoflustra flagellata* to *A. tenuis* in niche occupation and feeding activity (chapter 8,

see also Barnes & Clarke 1994) suggests that *N. flagellata* might similarly lack seasonality in growth, despite the strongly seasonal changes in resource and climate. Both these species apparently feed for the majority of the year, as has recently been found to be the case for a number of other Antarctic suspension feeding taxa studied (chapter 9, see also Barnes & Clarke 1995a); and at least one Antarctic bryozoan, *Arachnopusia inchoata*, has lophophores everted throughout the year (chapter 8). Clearly a variety of feeding and growth strategies exist among Antarctic bryozoans. Recent work on brachiopods and bivalve molluscs indicates that other Antarctic herbivores may also grow continuously throughout the year (L.S. Peck pers. com.). Annual growth rates expressed as either drymass or zooid production are quite variable between the species studied, ranging from slow (*A. tenuis*) to comparable with temperate species (*N. flagellata*). *Alloeflustra tenuis* grows quite slowly, reaching 1 gram of dry matter in approximately 16 years (back calculation using modelled growth), compared with 4 years in *Flustra foliacea*. If *N. flagellata* does have a similar pattern of annual growth to *A. tenuis*, its annual growth rate might not be too dissimilar from that of *F. foliacea*.

Cellarinella watersi has a slightly different morphology from these species, in having a heavily calcified skeleton. *Membranipora savartii*, a moderately calcified species from India has, however, been reported to have very fast growth rates, despite the high energy investment in skeletal material (McKinney & Jackson 1991). Expressed in terms of dry mass, the annual growth of *C. watersi* is similar to that of *Flustra foliacea*, but is very much lower when measured in terms of zooid production or organic (ash-free dry mass) growth. Since *C. watersi* does not grow throughout the year, the actual rate of growth, whilst growing in summer, will be very much faster than the mean annual rate.

The growth checks of *Cellarinella watersi*, which have been shown to be annual, enclose 'internodes' that vary in size with age. Growth in some years was found to be significantly higher than in others, independent of specimen age. Significant differences have also been found in both the magnitude and duration of the plankton blooms at Signy Island during the austral summer (Clarke *et al.* 1988). The discovery of high feeding efficiency and feeding saturation at low cell concentrations in the Antarctic bryozoan

Himantozoum antarcticum (Sanderson *et al.* 1994), coupled with the apparently long period of feeding effort (chapters 8 & 9) suggested the likelihood of a relationship with the duration of nanoplankton abundance rather than the actual magnitude of the blooms. The pattern of duration of the nanoplankton abundance in Borge Bay was found to parallel the relative growth pattern of *C. watersi* between the years 1989-1992 (the years for which most specimen growth data is available). Thus, the magnitude of growth may depend on the period of time that this particular fraction of the plankton occurs at sufficiently high enough levels of abundance to make feeding by bryozoans energetically advantageous.

Distinct annual growth lines are well documented in the shells of a variety of temperate bivalve molluscs both externally and internally (see Lutz & Rhoads 1980 for review). Such growth patterns in bivalves have enabled age determination and analysis of between year growth variation (Thompson *et al.* 1980, Tanabe 1988, Jones *et al.* 1989). Recently, a high degree of interannual variation was described in the growth rate of the bivalve *Yoldia notabilis* from Japan, which was positively correlated with annual water column chlorophyll a content (Nakaoka & Matsui 1994). The banding patterns found in some Antarctic brachiopods are also suspected to be annual, although the only study to date found that growth checks were produced at intervals of greater than one year (L.S. Peck, pers. com.)

The maximum age of any specimen of *Cellarinella watersi* was 9 years, but this probably reflects vulnerability to mechanical damage by currents at shallow sites. The largest specimens of *Alloeflustra tenuis* and *Nematoflustra flagellata* found at the sampling location appear to be about 26 years old, although specimens of these two species trawled from 150 m, around Signy Island, are larger and may be much older (chapter 6). The frequency of iceberg impact on Antarctic shallow water benthic communities ultimately restricts community development and possibly age (Richardson & Hedgpeth 1977, Peck & Bullough 1993, Barnes 1995 a,b), though there are as yet few firm data on the frequency of iceberg impact at different depths.

Erect bryozoans are abundant members of the benthic suspension feeding

communities characteristic of many areas of the Antarctic shelf (Bullivant 1961, 1967, Winston 1983, Winston & Heimberg 1988, Galéron *et al.* 1992) and in certain habitats completely dominate the epifaunal sessile taxa (Barnes 1995b). This study and studies of feeding in Antarctic bryozoans (Barnes & Clarke 1994, 1995a) suggest that several strategies may be employed by members of this fauna to cope with extreme food and environmental seasonality. One of these appears to be efficient feeding (and becoming saturated) at very low cell concentrations, and consequently being able to feed over a longer period and at a relatively low metabolic cost. Such a strategy results in growth throughout (or close to throughout) the year. This has produced annual growth increments which in some cases may be comparable with growth of similar organisms in temperate waters. Conversely, a brief period of intensive feeding and growth during the austral summer followed by winter starvation (Clarke 1988, Fenchel 1990) and possibly 'hibernation' (Gruzov 1977) may be used by others. The latter, very seasonal, strategy found in *Cellarinella watersi* is probably also adopted by other bryozoans similarly displaying obvious growth check lines. A recent study of other Antarctic suspension feeders suggests that those taxa which utilise the more seasonal microplankton fraction of primary productivity, such as holothurians (chapter 9, see also Barnes & Clarke 1995a), may also have a very brief summer period of activity and growth.

Predation: the influence of nudibranch molluscs

Introduction

The principal factors influencing mortality of Antarctic bryozoan colonies at Signy Island are probably overgrowth by superior competitors and ice abrasion. They may, however, experience a degree of predation both from incidental grazing (e.g. from fish) or as a main food source for groups such as pycnogonids and nudibranch molluscs. Of these latter two groups of predators, the nudibranchs are considerably easier to monitor for a number of reasons. Local, and indeed general, taxonomic knowledge of Antarctic nudibranchs is greater than pycnogonids, different species can be easily be recognised *in situ*, and most move very slowly.

Little more is known at the present time of the ecology of the Antarctic representatives of the nudibranchia than was known at the time of the species' initial descriptions at the turn of the century (Bergh 1884, Vayssière 1906, Eliot 1907). Taxonomic knowledge has recently increased substantially; a number of species have been redescribed and in some cases (e.g., *Austrodoris kerguelenensis*) species previously described as separate have been revised to constitute just one species (Wägele 1987b, 1989, 1990).

Some of the species which are locally abundant at Signy Island, such as *Austrodoris kerguelenensis* and *Tritionella belli*, have been described as generally common in the Southern Ocean and circumpolar in distribution (Wägele 1987a, 1989a). In contrast *Pseudotritonia gracilidens* Thiele, *Notaeolidia gigas* and *Charcotia granulosa* appear to be comparatively rare (see Wägele *et al.* 1995a, b). Prior to a redescription using specimens collected during this study *Charcotia granulosa* was only known from a single specimen (Wägele *et al.* 1995b).

The majority of nudibranchs in which the feeding ecology has been described, have been shown to be quite nutritionally specific. Such specificity in diet is also found within

whole nudibranch families. Thus for example nearly all tritoniids have soft coral or gorgonian prey (Thompson 1972, Gomez 1973). What little dietary information we have on Antarctic species stems from a study on stomach content analysis of preserved specimens by Wägele (1989) and some casual observations from the United States benthic programme at McMurdo Sound (Dayton *et al.* 1974, Dayton 1979). Such studies suggested that *Austrodoris kerguelensis* usually feeds on the hexactinellid sponges *Rosella* and *Scolymastra*, and that *Tritionella belli* feeds on the stoloniferan coral *Clavularia*.

In this chapter observations were recorded on the distribution of the better known *A. kerguelensis* and *T. belli*, as well as six lesser known species, with the aim of investigating diet (and in particular the overall influence on bryozoan populations) and the degree of specificity, depth range and small scale local distribution.

Materials and methods

Study site and species

Field observations were made, using SCUBA, at seven sites within Borge Bay over a period of eight months during 1992 and 1993. The sites were Porny Rock (≈ 3 m, depth), Bare Rock (≈ 5 m), Polynesia Point (≈ 7 m), Outer Island site 1 (≈ 11 m), Powell Rock (≈ 18 m), Outer Island site 2 (≈ 27 m) and Outer Island site 3 (≈ 36 m). These, with the exception of Outer Island site 3, were characterised by hard substratum communities as described in chapters 2-4. The deepest site, Outer Island site 3, was at the interface between sediment and bed rock or rock rubble. The observation area within each site approximated to 20 m².

Nine species of nudibranchs were observed in the study areas, eight of which were sufficiently abundant for the purposes of this study. The species were: *Tritonia antarctica* Eliot, *Tritionella belli* Eliot, *Pseudotritonia gracilidens* Thiele, *Charcotia granulosa* Vayssi re, *Austrodoris kerguelensis* Bergh and *Notaeolidia gigas* Eliot. Two further species of the family Aeolidae remain to be identified; this is a taxonomically difficult

family which has been little studied in the Southern Ocean.

Sampling

Observations were recorded at each site during June, August and October 1992 and January 1993. The observations therefore encompassed most of the environmental conditions experienced annually. All sites in June and August were characterised by typical 'winter' conditions of low particle flux, low light, minimal disturbance by currents, a sea water temperature of -1.8°C and the presence of sea-ice (Clarke *et al.* 1988). By October the sea ice had broken up, and sea water temperature, phytoplankton biomass and consequently particle flux had started to increase, to reach summer maxima at about the time of the January observations. Each site was surveyed over a submerged duration of about 30 minutes (each month), except the deepest, which had to be surveyed by two dives of shorter duration because of SCUBA safety considerations. The substratum or host/prey species underlying each nudibranch was noted and samples of substrata were collected and preserved for identification as far as possible.

Results

A total of 882 observations were made on the eight species, but the three least common species were represented by less than 35 observations each. *Notaeolidia gigas* was the only species observed at the shallowest site, but *Tritonia antarctica*, *Charcotia granulosa* and *Austrodoris kerguelensis* were all abundant at 5 m (Fig. 11.1). *Pseudotritonia gracilidens* was not observed shallower than 11 m and *Tritionella belli* not shallower than 15 m. *T. belli* was the only species of nudibranch observed to be more abundant at the deepest site (≈ 36 m). *T. belli* was also found in 100-300 m benthic trawls carried out in Orwell Bight, Signy Island, together with the circumpolar species *Aegires albus* Thiele (not seen at any of the monitored sites). *Notaeolidia gigas* was unusual in being abundant at the shallowest location (≈ 3 m), the only other nudibranch species seen at this depth was one of the two unidentified aeolids.

Tritonia antarctica and *Notaeolidia gigas* were observed on a wide range of potential prey, but most frequently on different types of red algae (Fig. 11.2a & 11.2e). The other six study species were each largely found in association with a particular taxon or prey item. Despite the (significant) frequency with which *N. gigas* was encountered on algae, this species was only observed to actually feed on large hydroids, probably *Tubulopora* sp.. The related species *Pseudotritonia gracilidens* and *Charcotia granulosa* were both found mostly on particular species of cheilostome bryozoans (Fig. 11.2c & 11.2d). In more than half of the observations on the species, *P. gracilidens* occurred on the outer colony margin of the abundant foliose bryozoan *Arachnopusia inchoata*. There are strong similarities in colouration and morphology between *P. gracilidens* and the margin of *A. inchoata*. In contrast, the nudibranch *Charcotia granulosa* was less camouflaged on the encrusting bryozoan *Beania erecta*. When introduced experimentally to laboratory colonies, the presence of nudibranchs triggered a retreat from the immediately surrounding bryozoan zooids of both *Arachnopusia inchoata* and *Beania erecta*, and clumps of ruptured zooids were later seen. Whilst the bryozoans *A. inchoata* and *B. erecta* are highly abundant and occupy large areas of substratum (Barnes 1995a,b), the predatory nudibranchs are comparatively rare and very small, such that a study of feeding in randomly selected colonies (chapter 8) found approximately 98 percent of zooids active within the areas photographed. The overall impact of predation on the populations of these two bryozoan species was thus presumably very small.

Tritonella belli principally occurred on and was observed *in situ* to eat the octocoral *Ascolepis* sp. (Fig. 11.2b). *Austrodoris kerguelenensis* occurred almost entirely on one particular and abundant species, the demosponge *Dendrilla antarctica* Topsent (demospongiae), in contrast to previous observations which found *A. kerguelenensis* feeding on Hexactinellid sponges at other locations (Odhner 1926, Dayton et al. 1974, Dayton 1979, Wägele 1989). The 140 specimens observed of the unknown aeolid species 1 were found entirely on the hydroids *Symplectoscyphus vanhoeffeni* Totton and *Symplectoscyphus glacialis* (Jäderholm) (Fig. 11.2f) together with egg masses assumed to be theirs. The other unknown aeolid species was found almost entirely on hydroids of the genus *Tubulipora* (Fig. 11.2g).

Figure 11.1

Total number of specimens of each nudibranch species found at each site. The seven sites, from 3-36 m are denoted on the horizontal axis. Note that the scale of the vertical alters between graphs because of the different levels of abundance between species. Many species were not recorded from one or more of the sites.

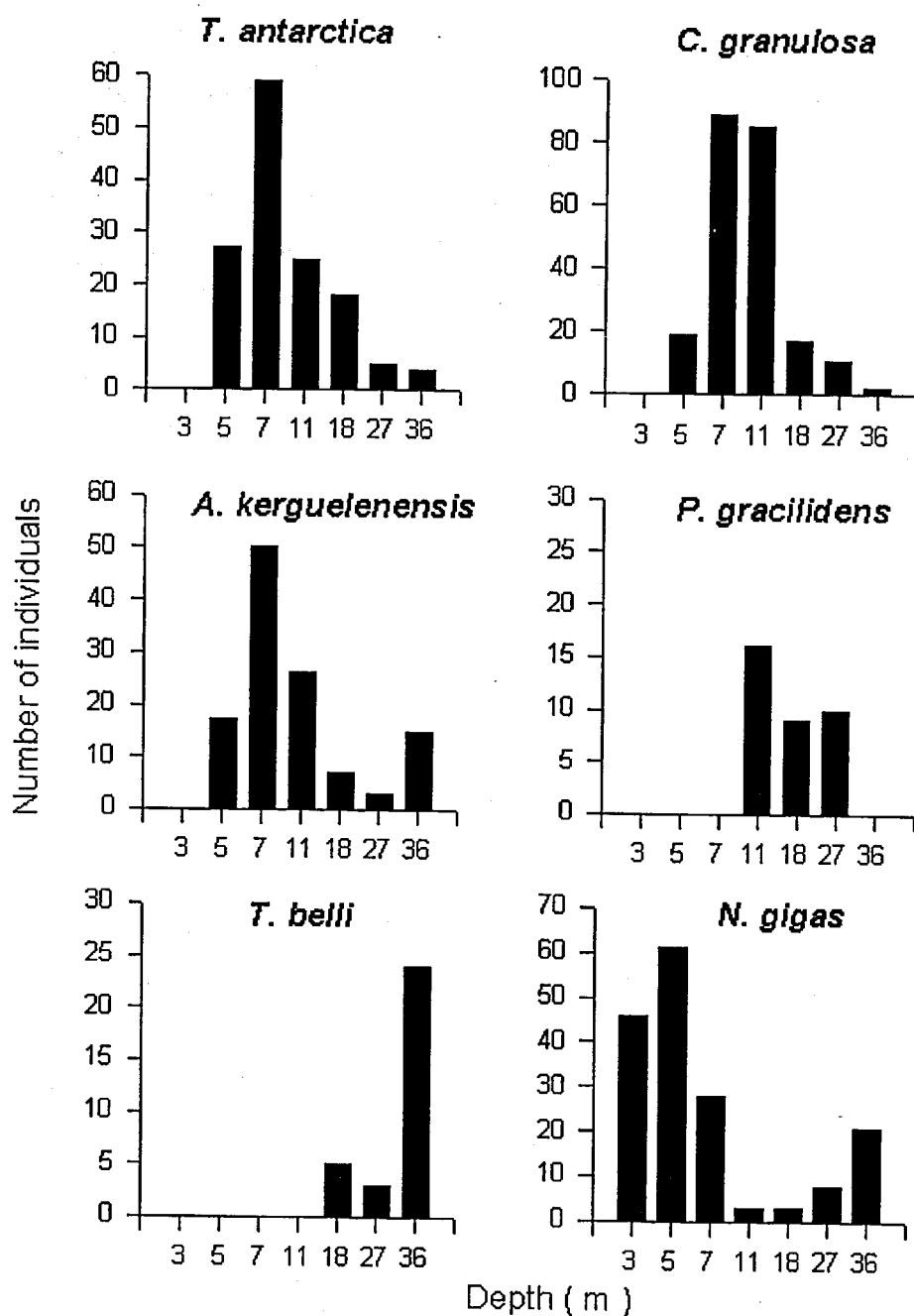


Figure 11.2

Total number of specimens of each nudibranch species found on each substratum type. Substratum abbreviations are; Brachiopod = *Liothyrella uva*, Polychaete = *Potamilla antarctica*, Octocoral 1 = *Ascolepis* sp., Octocoral 2 = *Thourella* sp., Hydroid 1 = *Tubulopora* sp., Hydroid 2 = *Symplectoscyphus* sp., Hydroid 3 = other hydroid genera, Sponge 1 = *Dendrilla antarctica*, Sponge 2 = other demosponge genera, Bryozoa 1 = *Beania erecta*, Bryozoa 2 = *Arachnopusia inchoata*, Bryozoa 3 = other bryozoans, Algae 1 = *Lithothamnion* sp., Algae 2 = other Rodophyta, Algae 3 = Phaeophyta.

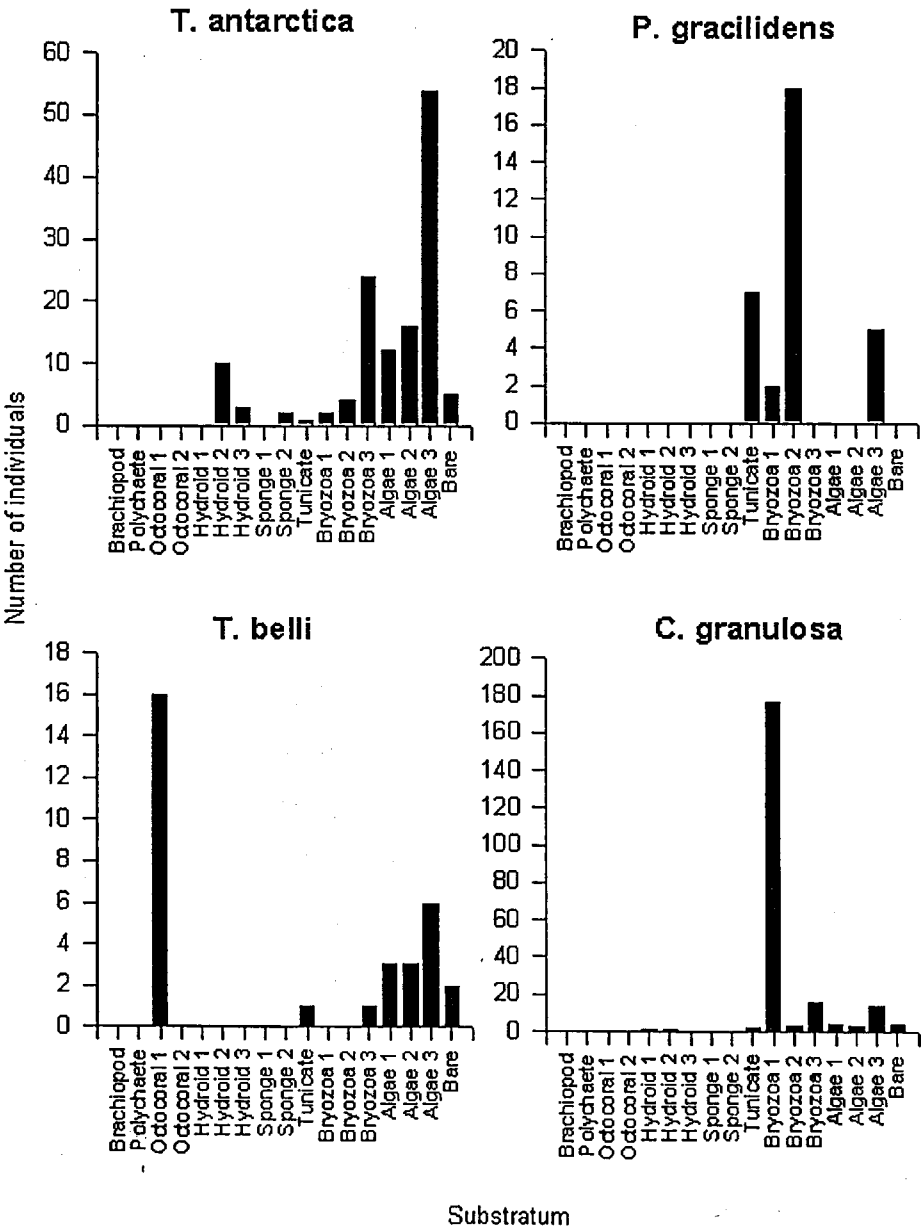
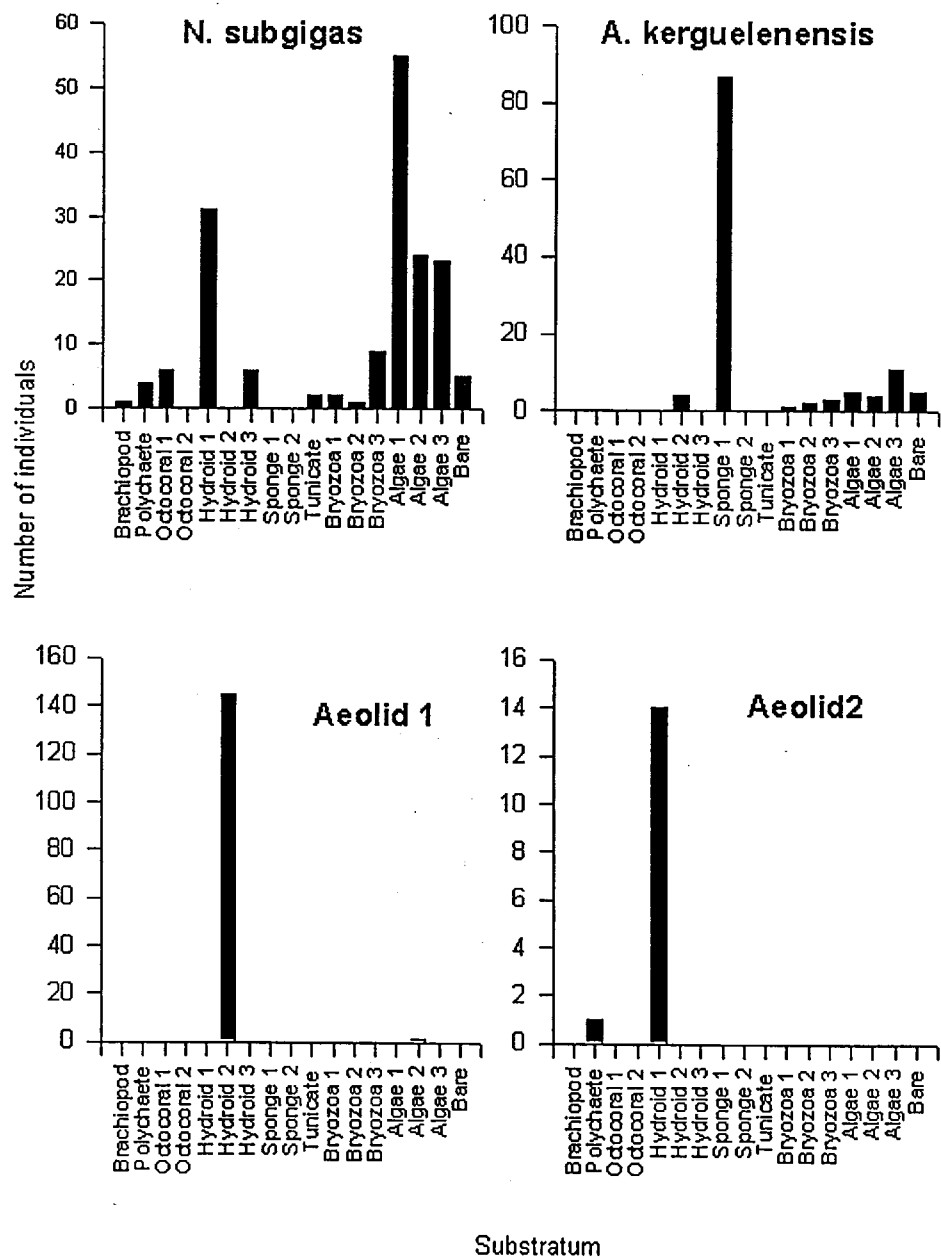


Figure 11.2b

Total number of specimens of each nudibranch species found on each substratum type. Substratum abbreviations are; Brachiopod = *Liothyrella uva*, Polychaete = *Potamilla antarctica*, Octocoral 1 = *Ascolepis* sp., Octocoral 2 = *Thourella* sp., Hydroid 1 = *Tubulopora* sp., Hydroid 2 = *Symplectoscyphus* sp., Hydroid 3 = other hydroid genera, Sponge 1 = *Dendrilla antarctica*, Sponge 2 = other demosponge genera, Bryozoa 1 = *Beania erecta*, Bryozoa 2 = *Arachnopusia inchoata*, Bryozoa 3 = other bryozoans, Algae 1 = *Lithothamnion* sp., Algae 2 = other Rodophyta, Algae 3 = Phaeophyta.



Discussion

Of the eight species of nudibranch molluscs found in the survey only two appear to feed predominantly on bryozoans. Both *Pseudotritonia gracilidens* and *Charcotia granulosa* were quite specific to the common cheilostome species *Arachnopusia inchoata* and *Beania erecta* respectively. *A. inchoata* and *B. erecta* are two of the most abundant bryozoans within the study locations and can occupy large proportions of available vertical hard substratum (chapters 2 & 3, see also Barnes 1995a,b). Neither populations of these two prey species, nor those of other locally abundant bryozoan species appear to be greatly influenced by predation.

The only nudibranch in which the observed distribution could obviously be explained by diet was *Pseudotritonia gracilidens*. The probable prey of *P. gracilidens*, the bryozoan *Arachnopusia inchoata*, rarely grew large in shallow water and was less abundant at the sites which were at the depth extremes of this study (chapters 2 & 3). Thus the observed absence of *P. gracilidens* from the extreme study depths could be linked directly to the abundance of *Arachnopusia inchoata*. The foliose bryozoan *Lageneschara lyrulata* is very similar to, and grows in the same areas as, *Arachnopusia inchoata*, but no specimens of *P. gracilidens* were observed on *Lageneschara lyrulata*, suggesting a strong diet specificity in *P. gracilidens*. The importance of the colouration and morphological resemblance between predator and prey for *P. gracilidens* was not clear.

Strong feeding specificity was also illustrated by *Tritionella belli* as no specimens were found on another octocoral (*Thourella*) which grew within the surveyed sites and amongst stolons of *Ascolepis*. Although *Ascolepis* is common, it is not encrusting and so does not form large unbroken expanses, thus in contrast to most of the other study species *T. belli* must search for food once a stolon has been consumed. This may be important in explaining the presence of individuals of *T. belli* on other substrata. Taxa, such as coralline algae, which are major space occupiers at sites would therefore be expected to have a proportion of 'searchers' (nudibranchs moving between food organisms) recorded at any instant.

The hydroid prey of *Notoaeolidia gigas* only occurs in clumps of small numbers of individuals with patchy distribution. The hydroids are small relative to the nudibranch and constitute a small biomass. Thus the presence of the majority of *N. gigas* specimens on a wide range of substrata, particularly algae, could be explained by the greater search time required compared with the other study species. The comparative increase in activity (search time) for *T. belli* and particularly *N. gigas* must have important metabolic and nutritional consequences. The study populations of *Tritonia antarctica* also covered a range of substrata, indicative of a similar feeding strategy to *T. belli* and *N. gigas*. *Tritonia antarctica* was the only study species for which the diet remains unknown, although an alternative explanation to the 'specific feeding, itinerant searchers' is one of omnivory, as has been found in just two nudibranch species to date (Wägele 1989).

The two other aeolid species were also found on a single hydroid species (different in the two aeolids), yet unlike *Notoaeolidia gigas* virtually no specimens were recorded on other substrates. The unknown aeolid species 2 fed on hydroids of the genus *Tubulipora* as did *N. gigas*, however the body size of the unknown aeolid was at least an order of magnitude smaller than *N. gigas*. A small clump of hydroids may therefore support the small aeolids for a proportionally greater period of time. Thus the ratio of prey biomass to predator biomass for these small aeolids on hydroid clumps probably approaches that for other larger study species, such as *Austrodoris kerguelensis*, on large tracts of prey in excess of a square metre. *Charcotia granulosa* is, at 15mm long, only about twice the size of the two unknown aeolid species and was, like these, rarely observed separate from its prey (the encrusting bryozoan *Beania erecta*).

This study has confirmed the diets of the circumpolar species *Notoaeolidia gigas* and *Tritoniella belli* suggested by the few field observations made (Dayton et al. 1974, Dayton 1979) and gut content analysis (Wägele 1989). Although *Austrodoris kerguelensis* was observed to have a highly specific sponge diet, as also observed during studies at other locations, it was a demosponge as apposed to the hexactinellid sponges reported elsewhere. Several other species studied here illustrated a high degree of diet specificity, as similar or closely related species to their prey were abundant in the same

localities, but remained untouched. With the exception of *Tritonia antarctica* whose dietary habits remain unknown, all the study species seemed to be specialists in feeding behaviour and as such fit into the existing categories in the ecological/dietary groupings proposed by Todd (1981).

The rich hard substratum communities on the submerged steeply sloping rock faces at Signy island contain a wide variety of suspension feeding taxa (Barnes 1995a,b). Some examples of these suspension feeders have been shown to feed for the majority of the year despite the intense seasonality of the environment (Barnes & Clarke 1994, 1995a). Survival may occur through efficiency at low food concentration (Sanderson *et al.* 1994) and low metabolic rates (Peck 1989). The survival strategy of slow moving Antarctic nudibranchs may be similar. All the study species feed on the most abundant species within the suspension feeding taxa at Signy, and those which are small in size relative to their prey (*Charcotia granulosa*, *Austrodoris kerguelensis* and the two aeolid sp.) apparently have little impact on prey populations. Such nudibranchs may have little cause to ever leave their host prey and in this study were rarely found on other substrata. With the exception of *A. kerguelensis* the high ratio of prey to predator size is caused by the nudibranch species being physically very small. All the study species which were found on a variety of substrates besides the suspected prey species were physically large in size. Thus the type of feeding strategy employed by Antarctic nudibranchs may largely be determined by physical size. So whilst large species such as *Notoaeolidia gigas* may travel in search of hydroids a fraction of their body size, such a strategy might energetically spell death to the physically smaller species which may not be able to afford the metabolic cost and predation risk of long journeys between prey items.

Section 4: General Discussion

General Discussion

Bryozoans have been recorded from virtually all aquatic habitats on earth, from freshwater rivers and lakes, through brakish-water lagoons to intertidal, sublittoral, shelf and deep sea marine environments. Many bryozoan classes, orders and genera are best or only known from fossils, and consequently much of the current work on this phylum comes from the field of palaeontology. Of the living specimens, intertidal and sublittoral bryozoans from temperate and tropical regions have received the most intensive study programmes, largely for logistic reasons, and therefore the majority of our knowledge of bryozoan ecology stems from these. One virtually unstudied region of the maritime world offers unrivalled opportunities for studying benthic communities away from anthropogenic influences, namely the Southern Ocean. Since the expeditions at the start of the century, this has been known to harbour some extremely dense and diverse assemblages of benthic suspension feeders, in particularly bryozoans. This region, the Southern Ocean, surrounds the Antarctic continent and forms 22% of the worlds oceanic water by surface area and therefore probably a similar area of seafloor. Even now only a few small marine localities have been examined in any detail and the ecology of many groups remain totally unstudied.

Bryozoans have not escaped scientific notice as they form such a significant proportion of or dominate the benthos which has been examined from around the continent over the last four decades (e.g., Belyaev & Uschakov 1957, Uschakov 1963, Bullivant 1967, White & Robins 1972, Moyano 1979, Voß 1988, Winston & Heimberg 1988, Galéron *et al.* 1992). Revealing such a presence was, with respect to bryozoans, largely the scope of such studies, but the extensive taxonomic work of Dr. P.J. Hayward and co-authors (Dr J.P. Thorpe & Prof J.S. Ryland) removed the major nonlogistic barrier for ecological studies. The novelty of ecological research on Antarctic bryozoans, particularly that which was undertaken *in situ*, meant the paths of investigation open to this thesis were broad. Originally the main aspect of ecology intended for investigation was seasonal and annual growth in a wide range of species and morphologies, but logistics changed the emphasis to that of distribution. The four main aspects of bryozoan ecology which have been covered by this thesis, namely distribution, competition, seasonality of feeding and

growth were thus decided in the field. The sequence, reflected in the order of chapters, reflects a logical flow from distribution to more specific ecology.

The distribution of bryozoans on both broad and fine scale was the most obvious point to begin such a thesis, as it not only gives an indication of how important bryozoans are locally relative to other benthic groups but is also the only area of overlap with previous ecological knowledge of Antarctic bryozoans. Rarely, and even then only in certain conditions, was encrusting benthic fauna found inhabiting the intertidal zone, as has also been found by researchers at other Antarctic intertidal localities (Hedgepeth 1971, Zamorano 1983, Rauschert 1991). The few species of bryozoans and hydroids present on the undersurfaces of rocks were found to experience severe extremes of both temperature and salinity (chapter 4, Barnes *et al.* in review). In the shallow sublittoral, however, bryozoans were extremely common on hard substrata of any type, and especially as colonists of other macroinvertebrates (chapter 6, Barnes & Clarke 1995b). Bryozoans were the dominant colonisers, in space occupied, of epifaunal molluscs and brachiopods as commonly found at lower latitudes, for both fossil (Ager 1961, Taylor 1979, Kesling *et al.* 1980) and living species (Doherty 1979, Hammond 1984, Keough 1984, Ward & Thorpe, 1991). Some more unusual substratum organisms were also colonised, including holothurians, isopods and even potential predators such as pycnogonids.

On abiotic substrata the overall abundance of bryozoans and other encrusting phyla changed with rock size, depth and rock surface profile, each of which suggested that the most important factor governing community development was disturbance and its frequency (chapter 4, Barnes & Rothery in review). Scour by floating ice and the winter build up of an icefoot around the intertidal zone is principally responsible for much disturbance in the nearshore marine environment at Signy Island, although wave action may also be important in rock turnover rates in shallow water. Bryozoans were found to be a major occupier of space at 4-40 m, particularly in frequently 'disturbed' conditions or ephemeral habitats such as small rocks and boulders and biotic substrata. The process of colonisation of available space appears to be very slow compared to those temperate or tropical regions which have been studied. Only deep into submarine caves have similar levels of colonisation ($\approx 5\%$ in

several years) been found at lower latitudes (Harmelin, 1985, 1986). The absence of certain locally common cheilostome species from the early developmental stages of such communities, the inverse relationship of abundance with overgrowth rank and the absence of many species from more developed communities, illustrated that not only is local diversity maintained by disturbance, but also that the pattern of succession appears to be facilitative and orderly. In the marine environment, both the maintenance of diversity by disturbance (Dayton & Hessler 1972, Oliver & Slatery 1985), and the mechanisms of succession (Odum 1969, Horn 1974, Greene & Schooner 1982, Todd & Turner 1986) have been much discussed and disputed over the last few decades. The input of information into such discussions from the Antarctic environment, which is very different from the much studied lower latitude marine environments and still relatively new to benthic ecological studies, must therefore be valuable.

Examination of competition between bryozoans and other taxa, and within bryozoan species is inevitably linked to the above studies of colonisation, distribution and abundance. Of the four most important encrusting faunal groups, bryozoans were found to overgrow spirorbid polychaetes and to be overgrown by sponges and tunicates. Similar results, of interactions between bryozoans and other such taxa, have been found at temperate and tropical latitudes (Stebbing 1973, Osman 1977, Keough 1984, Rubin 1985). The outcomes of bryozoan - bryozoan competition did not alter dramatically between sites or habitat stability (in contrast to cover and community composition, which did), but showed a marked difference in overgrowth abilities between species. The species could be clearly ranked according to overgrowth success, from a virtually complete dominant species to one which was nearly always overgrown. Thus on subjecting the resultant overgrowth scores to indices of transitivity (such as those proposed by Rubin 1982, and Tanaka & Nandakumar 1994) the assemblage was found to be hierarchically dominant. This is relatively unusual as interactions within most encrusting assemblages to have been studied are described as intransitive, or forming competitive networks (Jackson & Buss 1975, Jackson 1979, Rubin 1982, Turner & Todd 1994). This explains the monopolisation of large tracts of hard substratum at less disturbed areas within the sublittoral, observed at Signy Island (Barnes 1995a,b). Despite most species developing unique morphological

structures in such interactions, some morphological precursors (zooid height and colony growth form) for such a pronounced assemblage ranking were found (as also described at lower latitudes by Jackson 1979). In contrast to the predominantly decided outcomes of interspecific competition, nearly all the outcomes of intraspecific interactions between bryozoans were tied, some of which resulted in fusion between zooids of different colonies.

The mechanisms and dynamics of, and influences on feeding in a number of temperate bryozoans have recently received much attention by researchers. Such studies, under laboratory conditions, have determined feeding current velocities (Best & Thorpe 1983, 1986, 1993, Fisher 1989), ingestion rates (Okamura 1984, 1987, 1990, Hunter & Hughes 1993) and particle size or 'taste' selection (Okamura 1987, 1990, Fisher 1989, Best & Thorpe 1993). The first laboratory investigation of feeding in an Antarctic bryozoan (Sanderson *et al.* 1994) found a relatively high efficiency and saturation, in comparison to temperate bryozoans under similar conditions, at low concentrations of suspended cells (food). The present *in situ* studies of feeding duration, the first of their kind, found that most of the Antarctic bryozoan species investigated ceased feeding for only a few months a year, and that one species, *Arachnopusia inchoata*, had lophophores everted year round (Barnes & Clarke 1994, 1995a). Both the laboratory findings of Sanderson *et al.* (1994) and the *in situ* results reported in this thesis suggest a very different strategy from that traditionally conceived of as a long period of winter starvation (Clarke 1988, Fenchel 1990) and hibernation (Gruzov 1977) in polar suspension feeders. It is only recently that the measurements of phytoplankton standing crop, at Signy Island, has been size fractionated (Leakey *et al.* 1994). The duration of nanoplankton (2-20 μm) abundance, which is the size fraction on which bryozoans are believed to mostly feed (Winston 1977), is spread over a much longer period than that of the diatom dominated microplankton (20+ μm). Because the abundance of microplankton is an order of magnitude greater than that of the nanoplankton, the sharply seasonal microplankton dominates the overall pattern of chlorophyll standing crop to the extent that in unfractionated data the patterns of nano and picoplankton disappear, and thus the food supply for many benthic suspension feeders is not quite as intensely seasonal as was previously thought (Clarke 1988, Clarke *et al.* 1988). The polychaetes (*Potamilla* sp. and *Spirorbis* sp.) and hydroids (*Tubulipora* sp. and

Symplectoscyphus sp.) which were monitored exhibited a similar pattern of feeding activity to the bryozoans (Barnes & Clarke 1995a), in terms of duration and timing of activity changes, and probably utilise a similar size fraction of plankton. In contrast the holothurians (*Cucumaria* sp.), however, ceased feeding two months earlier than any other monitored suspension feeding taxa and for approximately five months of the year. As suspension feeding holothurians are known to feed principally on microplankton (Jørgensen 1966) and this fraction of the plankton is the most intensely seasonal (Leakey *et al.* 1994), the brevity of feeding duration compared with other taxa is intuitively reasonable.

No clear environmental cues to changes in feeding activity were obvious in any of the taxa monitored, although the similarity in timing between the two years of observations suggest that photoperiodicity may be a possibility. Alternatively the initiation of feeding activity in some bryozoans approximately coincided with the break up of sea-ice and the associated disturbance by increased water movement (Barnes & Clarke 1995a) and this, therefore, may act as an initiation cue, though sea-ice formation appeared to be unrelated to cessation of activity. From analysis of growth patterns, it seems likely that suspension feeders in temperate regions also cease feeding for at least a small period centered over winter (Stebbing 1971), but neither the exact duration or possible environmental cues to such changes in activity have received direct attention.

The bryozoans of the local shallow sublittoral were predominantly encrusting, but erect forms became increasingly abundant with depth (chapter 3, Barnes 1995b). In contrast to bryozoans of encrusting form, certain erect morphologies may provide a number of advantages for studies of growth, chiefly that they are easy to separate from substratum and so to collect. Whilst few studies have directly examined the growth of erect bryozoans at any latitude (e.g., Stebbing 1971, Keough 1989), only suggestions have been made on the degree or duration of growth in Antarctic bryozoans (Ryland 1976, Winston 1983). The erect species of bryozoans investigated in the present study exhibited quite different patterns of growth, both in terms of seasonality and zooidal production. *Alloeflustra tenuis*, about which, distribution, epibiota and feeding have already been discussed, seems to have little or no seasonality of growth. Recent work on other Antarctic suspension feeding taxa,

such as the brachiopods, has also found evidence of winter growth (L.S. Peck pers. comm. 1994). Year-round growth is perhaps surprising in view of the seasonality of feeding described of *A. tenuis* in chapter 8. Such an aseasonal growth pattern is also of interest when compared with the highly seasonal growth of the similar, but temperate, species *Flustra foliacea* (Stebbing 1971). The production of zooids and dry mass by *A. tenuis* is, however, lower than *F. foliacea*. If the Antarctic species *Nematoflustra flagellata*, which is similar to *A. tenuis* in both structure and ecology, has a similar annual pattern of growth to that of *A. tenuis*, then it may produce comparable growth to the temperate species. Why *N. flagellata* would grow so much quicker than *A. tenuis*, whilst being so similar in other aspects of biology, remains unclear at the moment. The above species are all only lightly calcified so most of this growth takes the form of extensive zooid production (at the upper margin of the colony). *Cellarinella watersi*, the other species for which growth was investigated, has a heavily calcified, rigid structure. Much of the growth of this species is consequently in the form of inorganic skeletal matrix and much fewer zooids are produced with time than the thin flexible flustrid species (chapter 10). In contrast to the flustrid species, the growth of *C. watersi* was highly seasonal, which resulted in the formation of check lines with changes in activity, separating the growth of each year. The discovery of such check lines being annual allowed not only aging of specimens and examination of age related growth but also investigation of interannual variations in growth. It was found that growth in some years is significantly higher than others and that these correlate with years in which the nanoplankton fraction had a greater than average duration of abundance (chapter 10). As with interspecific feeding seasonality, it seems there is probably a variety of strategies of growth employed between bryozoan species. At the study location (probably the shallowest location recorded for this type of bryozoan) the growth and age of *C. watersi* seems to be restricted by mechanical damage from freak currents.

This thesis describes some various basic aspects of ecology of bryozoans and how they compare or interact with other encrusting benthos in the sublittoral at Signy Island. Each area of investigation has opened many possibilities for future work by other researchers to gain a greater insight into the ecology of polar bryozoan communities.

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